University of Alberta

Localized permafrost peatlands in boreal western Canada: distributions, plant communities and peatland development

by

David W. Beilman

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

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Nov. 1, 2000.

DEDICATION

For my Dad, Wendlin H. J. Beilman, who first took me outdoors and showed me how to fully appreciate the natural world. Thanks, Dad, for teaching me everything I ever really needed to know.

ABSTRACT

Permafrost occurs in localized landforms within peatlands at its southern limit in western Canada. Extensive melt has shifted the southern limit north by 39 km on average and by as much as 200 km over the last 150 years. Localized permafrost peatlands cover 17,505 km^2 of Alberta, Saskatchewan and Manitoba, and occur in bogs and fens representing 37% of total bog cover, and 9% of total fen cover within their distribution. Field studies indicated that localized permafrost dynamics result in the creation of both the driest/most heavily forested and the wettest/most open conditions that occur in continental bogs. Plant communities, particularly bryophytes, responded strongly to these gradients, and vascular plant and bryophyte species richness increased by 49%, making localized permafrost bogs one of the most diverse peatland types in western Canada. Permafrost melt results in highly variable plant communities and developmental histories, due in part to varying degrees of disturbance (collapse) following melt.

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CHAPTER 1:
GENERAL INTRODUCTION

1.1 Permafrost and peatlands in western Canada

Permafrost is a thermal condition of surface earth materials that remain below 0°C for two or more years (Muller 1945). At the continental scale, the distribution of permafrost is considered in terms of continuity; the Continuous Permafrost Zone in Canada's north where permafrost occurs within all exposed land and is often hundreds of meters thick, and the Discontinuous Permafrost Zone where local factors determine the existence of perennially frozen ground that becomes increasingly thinner and less cold towards the south (Heginbottom 1995). Permafrost is an important aspect of the Canadian landscape, as the Permafrost Zones cover about half of Canada's landmass (French 1996). The boundary between these zones generally follows patterns of climate and roughly corresponds to the -8°C mean annual air isotherm (Brown 1960; Nelson 1989). In western Canada, this boundary runs from the northwest to the southeast from south of Inuvik, NWT to just south of Churchill, MB (Heginbottom 1995). South of this boundary, within the Discontinuous Zone, local factors that affect surface energy balances become increasingly important, as permafrost exists only where local terrain factors maintain perennially frozen ground. Such factors include landscape relief (affecting insolation), the albedo and conductivity of surface rock or mineral soil, vegetation, winter snow cover, and the presence of organic surface deposits or peat (French 1996). Within the Discontinuous Zone permafrost is most common in peatlands (Brown 1968). Permafrost reaches its southernmost limit (excluding alpine permafrost in the Rocky Mountains) in the boreal forest of Alberta, Saskatchewan and Manitoba (referred to here as continental western Canada). Here permafrost is limited exclusively to peatlands.

Peatlands are wetlands with greater than 40 cm of deposited peat where depressed decomposition rates result in the accumulation of organic material over time (Zoltai 1988). In western Canada, peatlands are typically dominated by bryophytes (though some fens are graminoid-dominated). Peatlands are a major component of the boreal continental western Canadian landscape, and cover 21% of the total land area of the prairie provinces (Vitt *et al.* 2000). This area contains two of the world's largest wetland areas, the southern portion of the Mackenzie River Basin (Nicholson *et al.* 1996) and the western portion of the Hudson Bay Lowlands (Zoltai *et al.* 1988).

In the Canadian Wetland Classification System, peatlands are classified based on their hydrology as bogs or fens (Zoltai 1988; Zoltai and Vitt 1995). Bogs are ombrogenous, oligotrophic peatlands that have surface waters and nutrients derived solely from atmospheric input. In continental western Canada, bog surfaces are elevated above the peatland water table, lack open pools, have *Sphagnum*-dominated ground cover elevated above the peatland water table, and are always treed by sparse *Picea mariana* (Mill.) BSP. Fens are geogenous, variably minerotrophic peatlands that have surface waters that are influenced by contact with mineral soils/substrata. Surfaces can be close to or at water table level, and fens can have open pools. Fens can be further subdivided based on their vegetation into poor and rich depending on the number of high-fidelity indicator species present (DuRietz 1949). The poor - rich division also corresponds to water chemistry gradients and nutrient availability (Sjörs 1952), as well as to the dominance of the ground layer by *Sphagnum* (poor fens) or brown mosses (mostly from the Amblystegiaceae – rich fens). Fens are also more physiognomically variable than bogs, and can be open, shrubby or treed.

Of these peatland types, permafrost has the greatest affinity for bogs. The dry, elevated *Sphagnum*-dominated bog surface peat can have a thermal conductivity an order of magnitude lower than wet peat (Brown and Williams 1972; Oke 1987), and water temperatures in bogs are consistently lower than those in the range of fen types (Vitt *et al.* 1995). The thermal characteristics of

ombrotrophic conditions are effective across spatial scales, including large bogs at the landscape level (kilometers), and small ombrotrophic areas that occur in fens at the local level (meters).

1.2 Peatlands and permafrost though the Holocene

Climate has been highly dynamic throughout the Holocene (the last 10,000 years) in western Canada. The early Holocene was characterized by glacial retreat and a spatially and temporally complex postglacial warm period that reached its maximum between 12000 and 6000 calendar years before present (BP) (Deevey and Flint 1957; COHMAP 1988; Anderson *et al.* 1989; Campbell and Campbell 1997) that prevented extensive peatland or permafrost development in the northern Canadian prairie provinces. Peatlands began forming in boreal continental western Canada between 10000 and 8000 years BP, with most expansion occurring since 8000 years BP (Halsey *et al.* 1998; Campbell *et al.* 2000). The discontinuous permafrost zone was likewise displaced north of its present location at 7000 years BP, and permafrost has aggraded in boreal peatlands since that time (Zoltai 1995). The maximum extent of permafrost has been hypothesized to have been reached more recently during the Little Ice Age (approx. 1550 – 1850 CE), and subsequent permafrost degradation has been attributed to natural climatic warming since then (Thie 1974; Vitt *et al.* 1994). Recent accelerated collapse rates calculated by dendrochronology (Engelfield 1994; Camill and Clark 1998) and aerial photography (Thie 1974; Kershaw and Gill 1979) have been attributed to anthropogenic climatic change. Recent results from the CCCma coupled climate model (combined effects of greenhouse gas concentrations and sulfate aerosol loading) predict that at least a 5°C increase in mean annual temperature will occur over the next century in continental western Canada (Boer *et al.* 2000). The response of peatland ecosystems to both the historical aggradation of permafrost and its continuing and potentially accelerating degradation has emerged as an important question (Gorham 1994), particularly within the

southern portion of the Discontinuous Permafrost Zone where the existence of permafrost is most sensitive to warmer temperatures.

1.3 Localized permafrost peatlands: terminology

Discontinuous permafrost in peatlands of subarctic and boreal Canada has long been recognized as occurring as two general landform types: large expansive areas of peatland underlain by permafrost called peat plateaus, and small isolated permafrost occurrences usually less than $100m^2$ in area (palsas) in otherwise unfrozen peatlands (Brown 1968; Zoltai 1971). Both landform types show evidence of permafrost degradation in continental western Canada. Areas of melt within peat plateaus are called collapse scars (Zoltai 1971) and collapsed localized permafrost landforms are called internal lawns (Vitt *et al.* 1994). Peat plateaus have low relief, usually elevated less than one meter above the surrounding unfrozen peatland, and cover up to many square kilometers (Zoltai 1972). Localized forms that occur as isolated small treed frost mounds in peatlands require more discussion and careful definition to avoid confusion in the use of the term 'palsa' (see review by Nelson *et al.* 1991).

The word 'palsa' was originally borrowed from the Lappish/Finnish and refers to 'a peat hummock with a frozen core rising out of the surface of a mire' (Seppälä 1988, page 249). While the original meaning is simply descriptive and non-genetic, its adoption into periglacial geomorphology has also included mineral cored mounds, and generally refers to treeless arctic/alpine forms that emerge out of saturated wetlands (Seppälä 1988). In Canadian subarctic and boreal peatlands small permafrost features of this scale have also been called palsas, though these 'invariably occur as islands or peninsulas in very wet fens or ponds' (Zoltai and Tarnocai 1975, page 34) as well as being differentiated from peat plateaus by their internal structure of frozen cores that extend into mineral substrata (Zoltai 1971). In addition, the Glossary of Permafrost and Related Ground Ice Terms (Harris *et al.* 1988) defines palsas as '...peaty permafrost mound(s) possessing a core of alternating layers of segregation ice

and peat or mineral soil material', further stating that '...ice segregation in mineral soil beneath peat is the process responsible for growth.' Visible ice layers are often absent in peat of localized frost mounds in boreal peatlands (Zoltai and Tarnocai 1975), and permafrost does not always extend into mineral soil under localized frost mounds (Zoltai and Tarnocai 1971) particularly at its southern limit.

Because localized permafrost in boreal western continental Canada is not restricted to wet fens (commonly occurring in ombrotrophic dry bogs as well (Vitt *et al.* 1994)), and the internal structure of every permafrost mound cannot be inventoried in regional surveys, using the term palsa adds confusion to the nature of permafrost in this region. Though a more general definition and usage for the term has been suggested (Nelson *et al.* 1991), I avoid the term palsa herein, instead referring to localized treed frost mounds in peatlands as simply 'localized permafrost.' However, this can be interchanged with 'wooded palsa' (cf. Zoltai 1972) if considered non-genetically and strictly as a morphological size description (*sensu* Washburn 1983). I use the phrase 'localized permafrost landform' in general reference to either existing localized treed frost mounds or internal lawns, and 'localized permafrost peatland' to describe peatlands with both/either of these features. Localized permafrost landforms can occur in either bogs or fens (Vitt *et al.* 1994), that I call 'localized permafrost bog' or 'localized permafrost fen'.

1.4 Localized permafrost bogs

Localized permafrost occurs in both bogs and fens in continental western Canada (Vitt et al. 1994). Localized permafrost aggradation results in the isolation of frost mound surfaces from the influence of peatland surface waters regardless of their hydrological nature (ombrotrophic or minerotrophic). Frost mound vegetation may therefore be similar whether these landforms occur in bogs or fens. In contrast, the degradation of localized permafrost results in internal lawns that have a very different vegetation and water chemistry character depending on the type of peatland they occur in. Internal lawns in localized

permafrost fens likely have surface water chemistry, plant communities and biogeochemical processes similar to the pool microhabitats of the undisturbed fen matrix, owing to the flow-through, minerotrophic nature of fen hydrology. Internal lawns in localized permafrost bogs, however, have a greater potential to have markedly different water chemistry, plant communities and biogeochemical process due to the ombrogenous hydrological nature of the bog matrix in which they occur, and the introduction of conditions and microhabitats that do not occur in continental bogs. Due to this potential for permafrost dynamics (permafrost aggradation and degradation) to influence the ecology of bogs to a greater degree than fens, localized permafrost bogs were investigated in the field.

1.5 Thesis objectives

Permafrost distributions have been dynamic at the southern limit of permafrost in western Canadian boreal peatlands over the last 500 years. The aggradation and degradation of localized permafrost has had substantial ecological effects on affected peatlands, though much remains to be learned about the magnitude, nature and implications of these changes (Gorham 1994). My objective in this thesis is to further the understanding of boreal permafrost dynamics and their influence on plant communities and peatland development in bogs. Herein, I use an existing database of wetland class coverages for continental western Canada, two years of summer field data, and peat core data to meet my specific objectives:

1) determine the spatial distribution of localized permafrost in peatlands across boreal Alberta, Saskatchewan and Manitoba relative to more extensive permafrost and climate/landscape characteristics (Chapter 2).

2) determine patterns of plant community and diversity change in localized permafrost bogs due to permafrost dynamics from three peatland study sites across western Canada (Chapter 3).

3) determine the nature of localized permafrost bog development following permafrost melt by reconstructing plant community and environmental change from macrofossil analysis of near-surface peat deposits (Chapter 4).

1.6 LITERATURE CITED

Anderson, T.W., Mathewes, R.W., and Schweger, C.E. 1989. Holocene climatic trends in Canada with special reference to the Hypsithermal interval. *In* Quaternary Geology of Canada and Greenland. *Edited by* R.J. Fulton. Geological Survey of Canada.

Boer, G.J., Flato, G., and Ramsden, D. 2000. A transient climate change simulation with greenhouse gas and aerosol forcing; projected climate for the 21st century. Climate Dynamics **16:** 427-450.

Brown, R.J.E. 1960. The distribution of permafrost and its relation to air temperature in Canada and the USSR. Arctic **13:** 163-177.

Brown, R.J.E. 1968. Occurrence of permafrost in Canadian peatlands. Proceedings of the Third International Peat Congress, Quebec. pp. 174-181.

Brown, R.J.E. and Williams, G.P. 1972. The freezing of peatlands. Technical Paper 381, Division of Building Research, National Research Council of Canada, Ottawa.

Camill, P. and Clark, J.S. 1998. Climate change disequilibrium of boreal permafrost peatlands caused by local processes. The American Naturalist **151:** 207-222.

Campbell, C. and Campbell, I.A. 1997. Calibration, review, and geomorphic implications of postglacial radiocarbon ages in southeastern Alberta, Canada. Quaternary Research **47**: 37-44.

Campbell, I.D., Campbell, C., Yu, Z., Vitt, D.H., and Apps, M.J. 2000. Millennial-scale rhythms in peatlands in the western interior of Canada and in the global carbon cycle. Quaternary Research **54**: 155-158.

COHMAP Members. 1988. Climatic changes of the last 18,000 years: observations and model simulations. Science **241:** 1043-1052.

Deevey, E.S. and Flint, R.F. 1957. Postglacial hypsithermal interval. Science **125:** 182-184.

DuRietz, G.E. 1949. Huvudenheter och huvugranser i svensk myrvegetation. Svenska Botaniska Tidskrift **43:** 274-309.

Engelfield, P.G.C. 1994. Rate of permafrost degradation in peatlands. M.Sc. Thesis. University of Alberta, Edmonton, Alberta. 33 pp.

French, H.M. 1996. The Periglacial Environment. Addison Wesley Longman, Essex, England.

Gorham, E. 1994. The future of research in Canadian peatlands: a brief survey with particular reference to global change. Wetlands **14**: 206-215.

Halsey, L.A., Vitt, D.H., and Bauer, I.E. 1998. Peatland initiation during the Holocene in continental western Canada. Climatic Change **40:** 315-342.

Harris, S.A., French, H.M., Heginbottom, J.A., Johnston, G.H., Ladanyi, B., Sego, D.C., and van Everdingen, R.O. 1988. Glossary of permafrost and related ground-ice terms. National Research Council of Canada Technical Memorandum 142, Ottawa, Canada.

Heginbottom, J.A. 1995. Canada - Permafrost, Plate 2.1, MCR 4177. *In* The National Atlas of Canada. National Resources Canada, Ottawa, Ontario.

Kershaw, G.P. and Gill, D. 1979. Growth and decay of palsas and peat plateaus in the Macmillan Pass - Tsichu River area, Northwest Territories, Canada. Canadian Journal of Earth Sciences **16:** 1362-1374.

Muller, S.W. 1945. Permafrost or perennially frozen ground and related engineering problems, special report, strategic engineering study 62, 2nd ed. United States Geological Survey, Washington.

Nelson, F.E. 1989. Permafrost zonation in eastern Canada: a review of published maps. Physical Geography **10:** 233-248.

Nelson, F.E., Hinkel, K.M., and Outcalt, S.I. 1991. Palsa-scale frost mounds. *In* Periglacial Geomorphology. *Edited by* J.C. Dixon, and A.D. Abrahams. John Wiley and Sons, London. pp. 305-325.

Nicholson, B.J., Gignac, L.D., and Bayley, S.E. 1996. Peatland distribution along a north-south transect in the Mackenzie River Basin in relation to climatic and environmental gradients. Vegetatio **126:** 119-133.

Oke, T.R. 1987. Boundary Layer Climates. Methuen and Co. Ltd., London.

Seppälä M. 1988. Palsas and related forms. *In* Advances in Periglacial Geomorphology. *Edited by* M.J. Clarke. John Wiley and Sons, Chichester. pp. 247-278.

Sjörs, H. 1952. On the relation between vegetation and electrolytes in northern Swedish mire waters. Oikos **2:** 241-258.

Thie, J. 1974. Distribution and thawing of permafrost in the southern part of the discontinuous permafrost zone in Manitoba. Arctic **27:** 189-200.

Vitt, D.H., Halsey, L A., Bauer, I.E., and Campbell, C. 2000. Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. Canadian Journal of Earth Sciences **37**: 683-693.

Vitt, D.H., Bayley, S.E., and Jin, T-L. 1995. Seasonal variation in water chemistry over a bog-rich fen gradient in continental western Canada. Canadian Journal of Fisheries and Aquatic Sciences **52:** 587-606.

Vitt, D.H., Halsey, L.A., and Zoltai, S.C. 1994. The bog landforms of continental western Canada in relation to climate and permafrost patterns. Arctic and Alpine Research **26:** 1-13.

Washburn, A.L. 1983. What is a palsa? Abhandlungen der Akademie der Sissenschaften in Gottingen, Mathermatisch-Physicalische Klasse **35:** 34-47.

Zoltai, S. 1971. Southern limit of permafrost features in peat landforms, Manitoba and Saskatchewan. Geological Association of Canada, Special Paper **9:** 305-310.

Zoltai, S.C. 1972. Palsas and peat plateaus in central Manitoba and Saskatchewan. Canadian Journal of Forest Research **2:** 291-302.

Zoltai, S.C. 1988. Wetland environments and classification. *In* Wetlands of Canada. Ecological Land Classification series, No. 24. *Edited by* National Wetlands Working Group. Polyscience Publications Inc., Montreal. pp. 1-23.

Zoltai, S.C. and Tarnocai, C. 1975. Perennially frozen peatlands in the western Arctic and Subarctic of Canada. Canadian Journal of Earth Sciences **12:** 28-43.

Zoltai, S.C. 1995. Permafrost distribution in peatlands of west-central Canada during the Holocene warm period 6000 years B.P. Géographie Physique et Quaternaire **49:** 45-54.

Zoltai, S.C. and Tarnocai, C. 1971. Properties of a wooded palsa in northern Manitoba. Arctic and Alpine Research **3:** 115-129.

Zoltai, S.C., Taylor, S., Jeglum, J.K., Mills, G.F., and Johnson, J.D. 1988. Wetlands of boreal Canada. *In* Wetlands of Canada. Ecological Land

Classification series, No. 24. *Edited by* National Wetlands Working Group. Polyscience Publications Inc., Montreal. pp. 97-151.

Zoltai, S.C. and Vitt, D.H. 1995. Canadian wetlands: environmental gradients and classification. Vegetatio **118:** 131-137.

CHAPTER 2:
LOCALIZED PERMAFROST PEATLANDS IN WESTERN CANADA: DISTRIBUTIONS AND DEGRADATION•

2.1 INTRODUCTION

Permafrost is a thermal condition of surface earth materials that remain below 0°C for two or more years (Muller 1945). At the continental scale, the distribution of permafrost is considered in terms of continuity; the Continuous Permafrost Zone in Canada's north where permafrost occurs within all exposed land and is often hundreds of meters thick, and the Discontinuous Permafrost Zone where local factors determine the existence of perennially frozen ground that becomes increasingly thinner and less cold towards the south (Heginbottom 1995). Within the Discontinuous Zone, permafrost is most common in peatlands (Brown 1968). Peatlands are bryophyte-dominated wetlands where low decomposition results in the accumulation of organic matter over time (Zoltai 1988). Peatlands are a major component of boreal and subarctic landscapes, covering about 21% of Alberta, Saskatchewan and Manitoba (referred to here as continental western Canada). Modern peatland distributions in western Canada follow climatic gradients (Halsey *et al.* 1997; 1998), and generally no peatlands occur where evapotranspiration exceeds precipitation (Gignac and Vitt 1994). Thus, peatlands are found in cooler climates that promote waterlogged soil conditions typical of the Discontinuous Permafrost Zone (Vitt *et al.* 1994). Peatlands can be divided into two general types based on hydrology; fens are geogenous peatlands that have surface waters that have been influenced by contact with mineral soil (ground or surface flow water), and bogs are ombrogenous peatlands that have surface waters derived from precipitation alone. Continental bogs in western Canada are characterized by oligotrophic nutrient status, tree cover of black spruce (*Picea mariana* [Mill.] B.S.P.), ground

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cover of *Sphagnum* spp. and a relatively dry surface elevated above the water table with a lack of open pools (Vitt *et al.* 1994). Fens are wetter, have a ground cover of brown mosses (rich fens) or *Sphagnum* spp. (poor fens), and are treed (black spruce and/or *Larix laricina* [Du Roi] K. Koch) or treeless (*Betula* or *Salix* shrubs or *Carex* spp.).

Peatland surface vegetation and soils promote the aggradation and maintenance of permafrost due to their dynamic physical and ecological effects on surface energy balances. Near-surface organic soils are insulative when dry during summer and become highly conductive when wet and frozen during the fall and winter - their thermal conductivity increasing by an order of magnitude (Brown and Williams 1972; Oke 1987) promoting deeper, colder winter freezes. The expansion of water upon freezing elevates surfaces above the surrounding peat surface and water table (Zoltai 1971) and can change ground cover vegetation from wetland *Sphagnum* spp. to non-wetland lichen and feathermoss communities (Belland and Vitt 1995), and promotes dense and tall growth of black spruce on localized frost mounds in the south (Zoltai and Tarnocai 1971). This dramatic vegetation change further maintains a negative or neutral energy balance through increased shade (forest cover) and ground surface albedo (lichen cover) during summer, as well as increased snow interception by the forest canopy during winter - thinning the ground snowpack that normally insulates the soil. These factors contribute to the aggradation and stability of perennially frozen soils, allowing them to occur at warmer latitudes and elevations than in other soil types or under different vegetation. Thus, at its southern limit in continental western Canada permafrost is limited exclusively to peatlands.

The permafrost-containing peatlands of subarctic and boreal Canada have long been recognized as occurring as two general types; large expansive areas of peatland underlain by permafrost called peat plateaus, and small isolated permafrost occurrences (usually less than 100 m^2 in area) in otherwise unfrozen

peatlands (Brown 1968; Zoltai 1971) that I call localized permafrost peatlands. Peat plateaus and localized permafrost have long been considered as morphological variations of the same process (Brown 1968), thus the occurrence of localized permafrost indicates a limit to local permafrost aggradation before peat plateau magnitude is attained due to interaction between climate and local factors (Seppälä 1994). This together with the location of localized permafrost at the southern limit of the discontinuous zone, makes localized permafrost in peatlands some of the most recently formed and most climatically sensitive perennially frozen ground in Canada.

Permafrost is degrading at many locations within the Discontinuous Permafrost Zone. Many authors have reported thermal degradation and disappearance of true palsas in the discontinuous zone for some time (Sollid and Sorbel 1974; Kershaw and Gill 1979; Brown 1980). In continental western Canada, peat plateaus and localized permafrost in peatlands also show evidence of extensive melt. Most peat plateaus have areas of internal degradation called collapse scars, and localized permafrost almost always has associated completely degraded forms termed internal lawns (Vitt *et al.* 1994). Internal lawns are treeless areas with carpet or lawn cover by *Sphagnum* spp. that typically have surfaces depressed about 50 cm below the surrounding non-permafrost peatland, often with tilted partially buried black spruce snags from the pre-existing frost mound (Vitt *et al.* 1994). The extensive degradation in continental western Canada, recently estimated to account for 9% (2627 km^2) of the total previously existing permafrost (Vitt *et al.* 2000a), has been attributed to natural climatic warming over the last 150 years since the end of the Little Ice Age (Halsey *et al.* 1995). The utility of monitoring characteristics and changes in such localized permafrost features as climate-change indicators has been advocated by numerous authors (Washburn 1980; Seppälä 1988; Solid and Sorbel 1998; Nelson *et al.* 1991). Given the sensitivity of localized permafrost to climate, as well as the important physical and ecological changes that have occurred within their distribution in the recent past, a detailed exploration of the distribution of

permafrost landforms in peatlands, particularly localized permafrost, is necessary to further understand the Canadian permafrost environment and how it is changing.

2.2.1 Objectives

Vitt *et al.* (1994) presented a preliminary, qualitative overview of localized permafrost and peat plateau distributions for continental western Canada. The data used by these authors were occurrences or counts of mapped peatland units within 15' latitudinal by 30' longitudinal gridcells, and summarized into classes that ranged from rare to abundant. Since then, these mapped peatlands have been digitized and summarized, and quantitative cover data for peatland types have become available. My goal in this chapter is to expand upon the initial work of Vitt *et al.* (1994) to determine the spatial distribution and to quantify cover of permafrost peatlands (peat plateau and localized permafrost peatland) at the regional scale, explore the relationship that these distributions have with climate and landscape, and determine how permafrost distributions have changed. Specifically, I will address the following questions: 1) What is the spatial distribution of a) the presence/absence of localized permafrost peatland relative to peat plateau, and b) landscape cover of localized permafrost peatland? 2) What climate/landscape factors are related to these distributions? and 3) What is the spatial distribution of complete degradation of localized permafrost (distribution of peatlands with internal lawns only, without treed frost mounds or peat plateau)?

2.2 METHODS

2.2.1 Localized permafrost peatland distribution

Wetlands were mapped from aerial photography (taken between 1949 – 1952) following the wetland classification described by Vitt *et al.* (1996). Information from the photos was transferred to 1:250,000 NTS base maps, digitized and summarized for 15' latitudinal by 30' longitudinal (NTS) gridcells in Arc/Info for Alberta and Saskatchewan and by the raster method (see Halsey *et al.* 1997) for Manitoba. Permafrost occurrence was inventoried as either 1) peatland completely underlain by permafrost (peat plateaus), or 2) as predominantly non-permafrost peatlands containing isolated permafrost landforms (localized permafrost peatlands). A minimum mappable unit of 0.6 km^2 ensured that only extensive permafrost peatlands were recorded as peat plateaus. Data are in the form of peatland area per gridcell for both permafrost landform types; peat plateau and localized permafrost peatland. Gridcells that occur within the Continuous Permafrost Zone of northern Manitoba (as mapped by Heginbottom (1995)) were not included.

To determine the spatial distribution of localized permafrost relative to peat plateau, gridcells were classified into four types by the presence/absence of permafrost peatland types and peatland coverage: 1) localized permafrost peatland only, 2) both localized permafrost peatland and peat plateau, with localized permafrost peatland dominant (localized permafrost peatland is ≥50% of total peat plateau and localized permafrost peatland cover), 3) both peat plateaus and localized permafrost peatland, peat plateaus dominant, and 4) peat plateau only. Cover values were assigned using five cover classes: < 0.49%, 0.5-4.9%, 5-14.9%, 15-24.9%, 25-50%. Classified gridcells were mapped in Arc/Info. The boundaries of the region of localized permafrost peatland occurrence were set by the northernmost and southernmost gridcell of the largely contiguous localized permafrost gridcells.

2.2.2 Climate and landscape factors

To further understand the controls on the spatial distribution of permafrost peatlands, a number of climate and landscape variables were estimated for the permafrost peatland area of continental western Canada. Variables were selected based on their importance to peatland and permafrost distributions and data availability for each peatland gridcell from published studies. Permafrost is a ground temperature phenomenon and distributions are related to climate. I include two climatic variables here, mean annual temperature and a summer aridity index. Mean annual temperature derived from climate normals (1951-1980) was linearly interpolated between available climate stations, correcting for elevation effects following Vitt *et al.* (1994). Because thermal conductivity of surface peat is strongly dependent on the soil moisture content, surface evapotranspiration rates are important to maintaining permafrost in summer. The combined effects of May through August precipitation and temperature are represented by a summer aridity index (based on precipitation - potential evapotranspiration) following Pettapiece (1995).

Three peatland variables were summarized for each gridcell, and included total peatland cover, the proportion of ombrogenous peatland, and maximum peat depth. Permafrost has an affinity for dry ombrotrophic peat at the local scale. To explore this relationship at the regional scale total peatland cover and the proportion of ombrogenous peatland to total peatland cover were estimated by the same method as permafrost landform cover from the wetland database. The maximum peatland depth occurring in each gridcell was compiled from numerous sources and consisted of 818 peatland sites and was otherwise interpolated where data were missing following Vitt *et al.* (2000b). Mineral soil texture was summarized for each gridcell based on a 5 point scale where smaller values represent smaller-grained soils (silts and clays) and larger values represent larger-grained soils (sandy soils) following Halsey et al. (1998). Gridcell topography was based on four relief classes ranging from level (1) to undulating (4) terrain following Halsey et al. (1998). To determine how climatic

and landscape character of gridcells in each permafrost landform class differed, data were submitted to canonical discriminant analysis (SAS 1990) following standardization (mean = 0, variance = 1) of all variables. The significance of climate/landscape variables in explaining localized permafrost peatland coverage was determined by stepwise multiple regression (Zar 1999).

2.2.3 Degradation

The spatial distribution of localized permafrost gridcells that contain only internal lawns (without frost mounds or peat plateaus), indicates the complete melt of permafrost that existed in the recent past. Spatial distribution of these cells demonstrate how distributions of localized treed frost mounds have changed.

2.3 RESULTS

2.3.1 Localized permafrost peatland distribution

Spatial distribution of gridcells classified by the presence/absence of permafrost landform types indicate a north to south latitudinal zonation with exclusive peat plateau occurrence in the north, typically exclusive localized permafrost peatland in the south, and a large area of overlap where both permafrost landform types co-occur (Fig. 2-1). The northern half (48%) of these permafrost cells contain peat plateaus exclusively, whereas exclusive localized permafrost peatland in the south account for 12% of the gridcells shown. The remaining permafrost cells have a co-occurrence of peat plateaus and localized permafrost containing peatland. One-third of all cells that contain permafrost have dominant or exclusive localized permafrost peatland. Outliers to the region of localized permafrost peatlands occur in the subarctic of northeastern Manitoba and at higher boreal elevations south of the zone in eastern Saskatchewan / western Manitoba (Fig. 2-1). Within the region, localized permafrost peatland covers 17,504 km^2, or 12.7% of total peatland area (Table 2-1). Cover is greatest in central and northeastern Alberta, northwestern Saskatchewan, and central

Manitoba, with the majority of cover being up to 5% of the land area in a broad band of occurrence (Fig. 2-2). About 56% of total localized permafrost peatland cover is fen, found mostly in central Manitoba. However, localized permafrost peatland cover is greater in bogs in Alberta and Saskatchewan (Table 2-1). When considered relative to cover by peatland type within the zone, 37.5% of total (non- peat plateau) bog area is localized permafrost bog. Localized permafrost fen accounts for 9.1% of total fen cover.

2.3.2 Climate and landscape factors

Permafrost peatland classes 1-3 (gridcells with localized permafrost peatland) are characterized by significantly different regional characteristics following canonical discriminant analysis ($F = 19.1$; $P < 0.0001$). Canonical axes 1 and 2 explain 32% and 3% of the variance in the climate and landscape data, with mean annual temperature and bog cover most strongly correlated with the first canonical axis (Table 2-2). The climate and landscape character of gridcells in these three classes show considerable overlap along the first axis in the ordination diagram (Fig. 2-3), suggesting a continuum of conditions between classes. Stepwise multiple regression of climatic and landscape variables against localized permafrost peatland cover per gridcell resulted in a model wherein only total peatland cover and mean annual temperature were significant (adjusted $r^2 = 0.316$; $F = 133.0$). Peatland cover accounted for the bulk of variability, as mean annual temperature increased model r^2 by less than 0.01.

2.3.3 Degradation

Of the gridcells with only localized permafrost peatland (Class 1 on Fig. 2-1), 40% of these have internal lawns only (without existing treed frost mounds). This complete permafrost degradation has occurred mainly in the south (Fig. 2-2), displacing the southern limit of permafrost north by an average of 39 km, though where internal lawns are found at higher elevations in boreal Saskatchewan and Manitoba, permafrost has moved by more than 200 km north.

2.4 DISCUSSION

2.4.1 Localized permafrost peatland distribution

The distribution of permafrost in Canada follows climate gradients, evident in the broadly latitudinal zonation of permafrost zones at the continental scale (Heginbottom, 1995). In this way, Continuous and Discontinuous Zone boundaries closely parallel mean annual temperature isotherms. This pattern is also seen within continental western Canada (Vitt *et al.*, 1994), where exclusive peat plateau occurrence in the north is replaced by increasing localized permafrost peatland in the south (Fig. 2-1). Distribution of permafrost peatland type and abundance forms the basis of Zoltai's (1995) sub-classification of discontinuous permafrost in peatlands. The total distribution of localized permafrost shown in Figure 2-1 spans his Sporadic and Localized Permafrost Zones. The region of localized permafrost peatland (Fig. 2-2) occurs as a broad band across the region. The greatest localized permafrost peatland cover generally occurs in the middle of this band, and decreases towards the north and south, due to marginal climatic conditions in the south and replacement by peat plateau in the north. Though more localized permafrost occurs in fens than in bogs (Table 2-1), much more of the total bog area has localized permafrost than the total fen area. This affinity for permafrost occurrence in bogs is due to bog surfaces elevated above the water table, their dry peat reducing groundwater temperatures below that of neighboring fens (Vitt *et al.* 1995). However, relatively dry rich fens are also common, especially in Manitoba, that also have elevated brown moss dominated surfaces. These dry fens are also prone to localized permafrost development.

2.4.2 Climate and landscape factors

As a thermal condition of surface material, permafrost is closely related to climate. The limits of the Discontinuous Zone have been expressed in terms of mean annual temperature, occurring between about -8.3°C (Zoltai 1995) and 0°C (Vitt *et al.* 1994) mean annual isotherms. Mean annual temperature is the most

strongly correlated variable to canonical axis 1 (Table 2-2), that best separates the permafrost peatland classes (Fig. 2-3). This indicates that overall coldness strongly affects the occurrence of permafrost peatland types, and that climate (specifically temperature), is an underlying factor that determines permafrost peatland distribution at the regional scale. Thus, colder regions can develop extensive peat plateaus, whereas warmer regions have a climatically imposed limit on landform development, and are conducive to aggradation of localized permafrost only. Seasonal precipitation also affects permafrost aggradation, maintenance and degradation. Wet peat has a thermal conductivity an order of magnitude greater than dry peat (Brown and Williams 1972), and high summer precipitation and flooding have degraded small permafrost lenses in Finnish Lapland wetlands (Seppälä 1994). Summer aridity was weakly but significantly correlated to canonical axis 1 (Table 2-2). This relationship likely has to do with the importance of aridity to permafrost maintenance at the southern limit of localized permafrost where aridity is highest, and promotes dry insulative peatland surfaces during the thaw season. Winter precipitation as snowfall, although not included in our analyses, also has an important affect on permafrost. The reduction of winter snowpack has been shown to be a limiting factor for permafrost aggradation in discontinuous zone wetlands (Seppälä 1994). This can occur at the very local scale by wind scour of higher microrelief in hummocky terrain or redistribution of snow by wind in treeless wetlands. In treed wetlands dense tree cover has a similar effect, intercepting much snowfall within living forest canopies (Zoltai and Tarnocai 1971).

Landscape factors that include peatland cover, peatland type (bog proportion of total cover), and mineral soil texture also show differences between permafrost peatland classes. Permafrost distribution is related to peatland distribution, as permafrost is found most commonly in peatlands within the Discontinuous Zone and is restricted exclusively to peat in the south. The correlation of peatland cover variables to canonical axis 1 demonstrates that the landform gradient is also limited by the extent of peatland area, especially at the

climatic limits of its occurrence. The amount of bog relative to total peatland cover in an area (gridcell) is more closely correlated to axis 1 than total peatland cover (Table 2-2), as ombrotrophic peatlands in the north of the provinces are almost exclusively peat plateau. Surface mineral soil texture shows hydraulic conductivity from low (clayey soils) to high (sandy soils). Increasing hydraulic conductivity has been associated with the occurrence of minerotrophic peatlands in Manitoba (Halsey *et al.* 1997) and Minnesota (Glaser 1992). The negative correlation of soil texture to axis 1 reflects the high abundance of fen peatland in the south of the zone of localized permafrost peatland occurrence, where localized permafrost is dominant or exclusive. Farther north peat plateaus begin to dominate and ombrotrophic conditions become more common, seen in the positive correlation of proportion bog to axis 1 (Table 2-2).

The variation in cover of localized permafrost peatland is best explained by total peatland cover, and to a much lesser degree by mean annual temperature. The bog proportion of total peatland cover is less important than total peatland area in this case. The high cover values of fen peatland within the distribution of exclusive or dominant localized permafrost peatland (class 1 and 2 gridcells) results in more localized permafrost fen than localized permafrost bog. Even though permafrost has a demonstrable affinity for bogs, localized permafrost aggradation is facilitated by dry microhabitats in fens. These include hummocky microrelief created by common peatland bryophytes such as *Sphagnum* spp. and *Tomenthypnum nitens* (Hedw.) Loeske, and dry ridges (strings) separating wet pools (flarks) in patterned fens. When regressed against coverage of localized permafrost landforms, climate is a poor explanatory variable. Part of this weak relationship is due to some non-linear response of localized permafrost peatland area to climate, since cover decreases in colder areas when localized permafrost is replaced by peat plateau. However, the majority of data for localized permafrost peatland cover per gridcell is less than 5% and spans the range of mean annual temperatures for these gridcells, implying that most of the variability in cover is controlled by other factors (i.e.

peatland cover). Altogether, this suggests that climate is an important factor in determining whether permafrost develops into expansive landforms or is limited to localized landforms. In areas where climate supports localized permafrost, cover is largely a function of available peatland area.

Although climate and landscape factors explain much of the presence/absence of permafrost landform types as well as the extent of localized permafrost at the regional scale, much variability remains unexplained. In continental western Canada the distribution of permafrost landform types, and the extent of peatlands containing landforms at their climatic limits such as localized permafrost, presumably reflect climatic patterns that existed during permafrost aggradation, i.e. during the Little Ice Age. While the Little Ice Age is expected to have been about 1°C colder than present mean annual temperatures in the region (Vitt *et al.* 1994), this cold period has been shown to have been asynchronous and of varying intensity worldwide (Bradley and Jones 1992). It is also possible that the climatic conditions and weather patterns of the Little Ice Age could have been substantially different than modern climate, as has been implicated as the cause of past dramatic weather changes in Churchill, Manitoba (Scott *et al.* 1988). Thus, even though modern climate is an important variable explaining the presence/absence of peat plateaus and localized permafrost in peatlands, some unexplained variability in our analyses may partially be due to climate data that inaccurately represent aggradation conditions. The inclusion of additional regional scale variables could likely explain more variation, however factors that operate locally also have a strong effect on permafrost peatland type and coverage. Camill and Clark (1998) showed that maintenance of relict permafrost is controlled by complex local factors that operate on a landform-to-landform scale. The large region of peat plateau and localized permafrost peatland co-occurrence, and that only certain peatlands or parts of peatlands have permafrost supports the importance of local factors and processes. Though climate and landscape impose regional thresholds, local factors are influential in

dictating the aggradation and degradation of permafrost at the southern limit of the discontinuous zone.

2.4.3 Degradation

Permafrost has been dynamic in its distribution in continental western Canada through the climatic changes of the Holocene. Zoltai (1995) tentatively demonstrated that at 6,000 years BP, permafrost zones were up to 500 km north of their current position. The Little Ice Age was the most extensive cold period since Late Wisconsinan deglaciation, evident in the most extensive glacial advances of the Holocene in the Canadian Rockies (Grove 1988; Luckman 1986), and tree ring records from Alberta (Case and McDonald 1995). It has been proposed that permafrost reached its maximum Holocene extent during this time, and account for much of the localized permafrost aggradation at the southern limit (Halsey *et al.* 1995). Dendrochronological dating of melt events show that degradation was initiated in the last 100 years (Vitt *et al.* 1994), which is synchronous with the amelioration of climate since the Little Ice Age (Thie 1974; Vitt *et al.* 1994). The spatial distribution of internal lawns shows that degradation has occurred throughout the zone of localized permafrost peatland occurrence (Vitt *et al.* 1994). This melting can be complete, with 40% of gridcells with only localized permafrost peatland (Class 4 on Fig. 2-1) having internal lawns only. The predominant distribution of completely degraded permafrost at the southern limit of permafrost demonstrates that climate warming is responsible for changes in permafrost distribution. The distribution of existing treed frost mounds has been highly dynamic over a relatively short period of time within the zone of localized permafrost peatland occurrence. Further study of localized permafrost landforms is important due to their utility as climate indicators, as well as to further understand the environmental consequences of ongoing permafrost melt in the boreal forest.

2.4.4 Conclusions

As a result of extensive inventory of peatland landforms and comparison to climate/landscape within continental western Canada, I demonstrate here that:

1. Permafrost landform occurrence as either peat plateaus or localized permafrost peatland is distributed in latitudinally-oriented bands of occurrence with peat plateaus only in the north, typically localized permafrost only in the south, separated by extensive overlap or co-occurrence of landform types.

2. Localized permafrost peatlands (peatlands with treed frost mounds and/or internal lawns) cover 17,505 km^2 in a zone of occurrence within the boreal forest of continental western Canada, concentrated in north central and northeastern Alberta, northwestern Saskatchewan and central Manitoba. Localized permafrost occurs in both fen and bog: localized permafrost fen covers 9,868 km^2 in this zone, localized permafrost bog covers 7,636 km^2.

3. Climate and peatland area are the most important regional factors for the occurrence of permafrost landform types as well as the extent and distribution of localized permafrost peatlands. At the regional level, climate controls permafrost development into either extensive peat plateau or localized frost mounds. In climates where localized permafrost peatlands occur, their regional coverage is mostly a function of peatland area. Local factors are responsible for short-term temporal dynamics at the site level.

4. Localized permafrost in peatlands is the most recently formed and the most climatically sensitive permafrost in the Discontinuous Zone. The continuing degradation of permafrost has moved the southern limit of permafrost north by an average of 39 km, and as much as 200 km over the last century.

Table 2-1. Summary of total permafrost landform and peatland type cover (km^2) by province for the zone of localized permafrost peatland occurrence (as shown in Fig. 2-1).

	ALBERTA	SASKATCHEWAN	MANITOBA	TOTAL
Peat plateau	3,439	709	11,795	15,943
Localized permafrost peatland	6,451	2,328	8,726	17,505
Localized permafrost bog	3,972	1,868	1,796	7,636
Localized permafrost fen	2,479	460	6,929	9,868
Total bog (non- peat plateau)	8,755	6,663	4,934	20,352
Total fen	37,301	24,438	46,308	108,047

Table 2-2. Results of canonical discriminant analysis: Pearson correlation coefficients for climate/landscape characteristics and canonical axes 1 and 2. *denotes significance ($P < 0.05$).

FACTORS	AXIS 1	AXIS 2
Mean annual temperature	-0.83*	-0.36*
Summer aridity	-0.27*	-0.09*
Total peatland cover	0.27*	-0.19*
Bog proportion	0.62*	0.01
Maximum peat depth	-0.02	0.24*
Topography	-0.03	-0.04
Mineral soil texture	-0.34*	0.81*
Squared canonical correlation	*0.32*	*0.03*

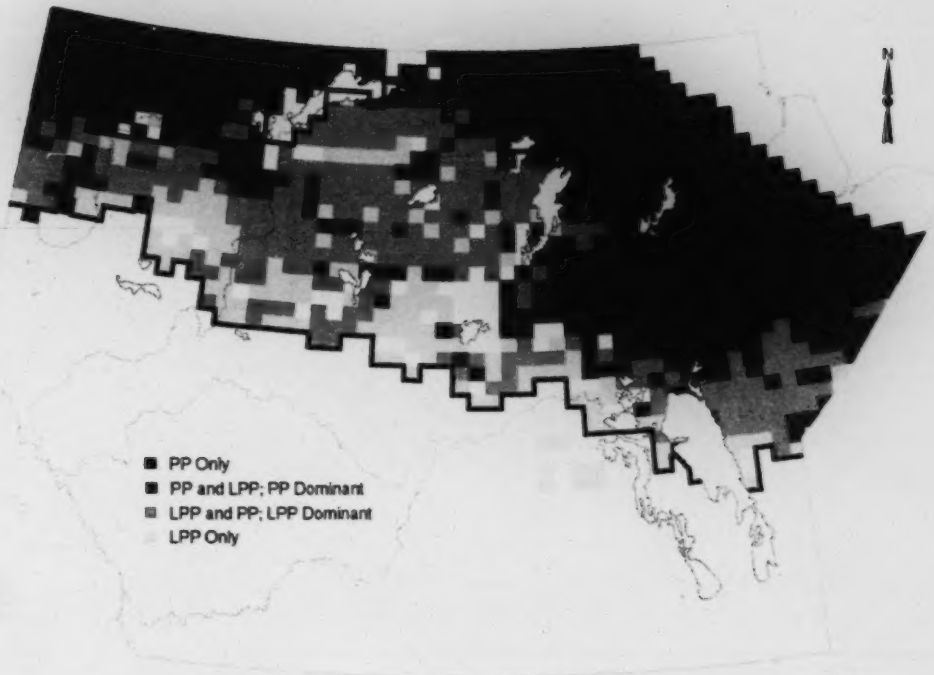


Fig. 2-1. Distribution of permafrost landforms in boreal continental western Canadian peatlands by landform class. PP = peat plateau, LPP = localized permafrost peatland. The northern and southern limits of the zone of localized permafrost peatland occurrence is demarcated by heavy lines. Cells within the Continuous Permafrost Zone (Heginbottom 1995) of northeastern Manitoba are excluded.

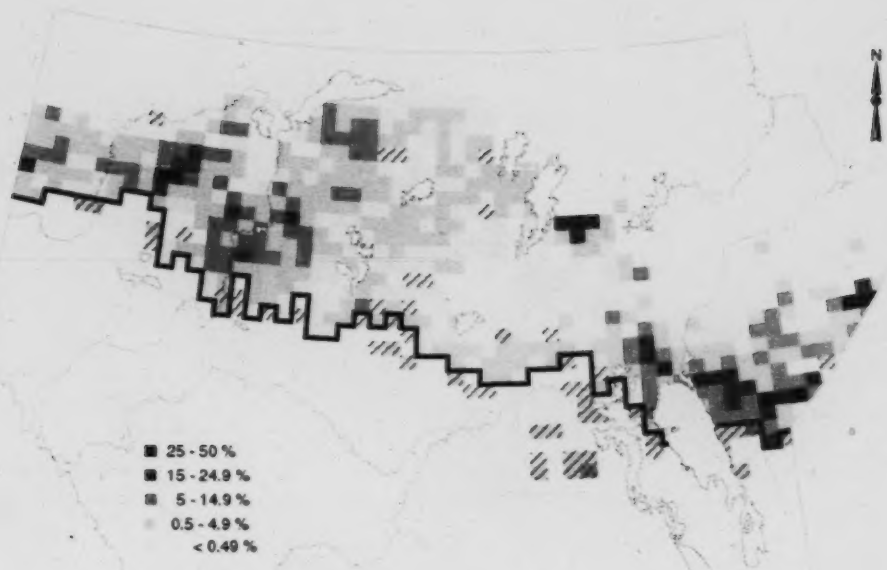


Fig. 2-2. Cover of localized permafrost peatland expressed as percentage of total peatland area per gridcell. Hatched gridcells show localized permafrost peatlands with internal lawns only. The modern southern limit of permafrost is shown by the heavy line.

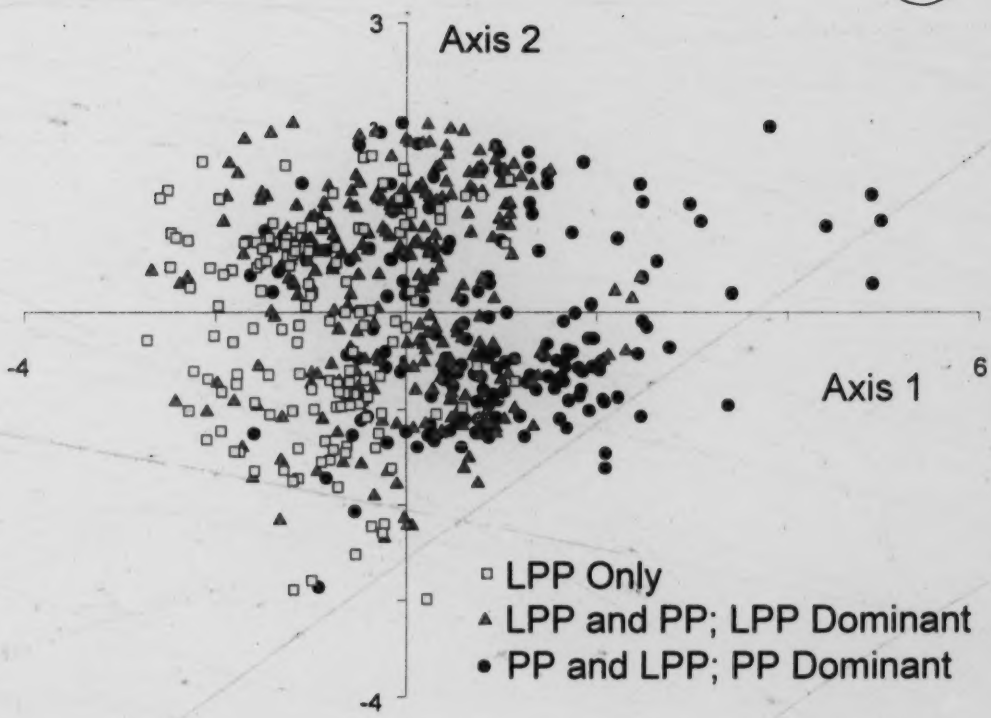


Fig. 2-3. Results of canonical discriminant analysis of climate/landscape characteristics comparing permafrost peatland classes 1-3 (localized permafrost peatland). Canonical axes 1 and 2 are plotted. PP = peat plateau, LPP = localized permafrost peatland.

2.5 LITERATURE CITED

Belland, R.J. and Vitt, D.H. 1995. Bryophyte vegetation patterns along environmental gradients in continental bogs. Écoscience **2:** 395-407.

Bradley, R.S. and Jones, P.D. 1992. Climate since A.D. 1500. Routledge, New York.

Brown, G. 1980. Palsas and other permafrost features in the lower Rock Creek valley, west-central Alberta. Arctic and Alpine Research **12:** 31-40.

Brown, R.J.E. 1968. Occurrence of permafrost in Canadian peatlands. Proceedings of the Third International Peat Congress, Quebec. pp. 174-181.

Brown, R.J.E. and Williams, G.P. 1972. The freezing of peatlands. Technical Paper 381, Division of Building Research, National Research Council of Canada, Ottawa.

Camill, P. and Clark, J.S. 1998. Climate change disequilibrium of boreal permafrost peatlands caused by local processes. The American Naturalist **151:** 207-222.

Case, R.A. and MacDonald, G.M. 1995. A dendroclimatic reconstruction of annual precipitation on the western Canadian prairies since A.D. 1505 from *Pinus flexilus* James. Quaternary Research **44:** 267-275.

Gignac, L.D. and Vitt, D.H. 1994. Responses of northern peatlands to climate change: effects on bryophytes. Journal of the Hattori Botanical Laboratory **75:** 119-132.

Glaser, P.H. 1992. Peat Landforms. *In* The Patterned Peatlands of Minnesota. *Edited by* H.E. Wright, B.A. Coffin, and N.E. Aaseng. The University of Minnesota Press, Minneapolis. pp. 3-14.

Grove, J.M. 1988. The Little Ice Age. Methuen and Co., New York.

Halsey, L.A., Vitt, D.H., and Bauer, I.E. 1998. Peatland initiation during the Holocene in continental western Canada. Climatic Change **40:** 315-342.

Halsey, L.A., Vitt, D.H., and Zoltai, S.C. 1995. Disequilibrium response of permafrost in boreal continental western Canada to climate change. Climatic Change **30:** 57-73.

Halsey, L.A., Vitt, D.H., and Zoltai, S.C. 1997. Climatic and physiographic controls on wetland type and distribution in Manitoba, Canada. Wetlands **17:** 243-262.

Heginbottom, J.A. 1995. Canada - Permafrost, Plate 2.1, MCR 4177. *In* The National Atlas of Canada. National Resources Canada, Ottawa, Ontario.

Kershaw, G.P. and Gill, D. 1979. Growth and decay of palsas and peat plateaus in the Macmillan Pass - Tsichu River area, Northwest Territories, Canada. Canadian Journal of Earth Sciences **16:** 1362-1374.

Luckman, B.H. 1986. Reconstruction of Little Ice Age events in the Canadian Rocky Mountains. Géographie Physique et Quaternaire **40:** 17-28.

Muller, S.W. 1945. Permafrost or perennially frozen ground and related engineering problems, special report, strategic engineering study 62, 2nd ed. United States Geological Survey, Washington.

Nelson, F.E., Hinkel, K.M., and Outcalt, S.I. 1991. Palsa-scale frost mounds. *In* Periglacial Geomorphology. *Edited by* J.C. Dixon and A.D. Abrahams. John Wiley and Sons, London. pp. 305-325.

Oke, T.R. 1987. Boundary Layer Climates. Methuen and Co. Ltd., London.

Pettapiece, W.W. 1995. Land Suitability Rating System for Agricultural Crops: 1.Spring-seeded small grains. Technical Bulletin 1995-6E. Centre for Land and Biological Resources Research, Agriculture and Agri-Food Canada. Ottawa, Canada.

SAS. 1990. SAS/STAT User's Guide, Version 6, Fourth Edition, Volume 2. SAS Institute Inc., Cary, N.C., U.S.A.

Scott, P.A., Fayle, D.C.F., Bentley, C.V., and Hansell, R.I.C. 1988. Large-scale changes in atmospheric circulation interpreted from patterns of tree growth at Churchill, Manitoba, Canada. Arctic and Alpine Research **20:** 199-211.

Seppälä M. 1988. Palsas and related forms. *In* Advances in Periglacial Geomorphology. *Edited by* M.J. Clarke. John Wiley and Sons, Chichester. pp. 247-278.

Seppälä, M. 1994. Snow depth controls palsa growth. Permafrost and Periglacial Processes **5:** 283-288.

Sollid, J.L. and Sorbel, L. 1974. Palsa bogs at Haughtjornin, Dovrefjell, south Norway. Norsk Geografisk Tidsskrift **28:** 53-60.

Sollid, J.L. and Sorbel, L. 1998. Palsa bogs as climate indicator-examples from Dovrefjell, South Norway. Ambio **27:** 287-291.

Thie, J. 1974. Distribution and thawing of permafrost in the southern part of the discontinuous permafrost zone in Manitoba. Arctic **27:** 189-200.

Vitt, D.H., Bayley, S.E., and Jin, T.-L. 1995. Seasonal variation in water chemistry over a bog-rich fen gradient in continental western Canada. Canadian Journal of Fisheries and Aquatic Sciences **52:** 587-606.

Vitt, D.H., Halsey, L.A., Bauer, I.E., and Campbell, C. 2000b. Spatial and Temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. Canadian Journal of Earth Sciences **37:** 683-693.

Vitt, D.H., Halsey, L.A., and Zoltai, S.C. 1994. The bog landforms of continental western Canada in relation to climate and permafrost patterns. Arctic and Alpine Research **26:** 1-13.

Vitt, D.H., Halsey, L.A., and Zoltai, S.C. 2000a. The changing landscape of Canada's western boreal forest: the current dynamics of permafrost. Canadian Journal of Forest Research **30:** 283-287.

Vitt, D.H., Halsey, L.A., Thormann, M.N., and Martin, R. 1996. Peatland inventory of Alberta. Alberta Peat Task Force, Network of Centres of Excellence in Sustainable Forest Management Grant, University of Alberta, Edmonton, Alberta.

Washburn, A.L. 1980. Permafrost features as evidence of climatic change. Earth-Science Reviews **15:** 327-402.

Washburn, A.L. 1983. What is a palsa? Abhandlungen der Akademie der Sissenschaften in Gottingen, Mathermatisch-Physicalische Klasse **35:** 34-47.

Zar, J.H. 1999. Biostatistical Analysis. Prentice Hall, New Jersey.

Zoltai, S. 1971. Southern limit of permafrost features in peat landforms, Manitoba and Saskatchewan. Geological Association of Canada, Special Paper **9:** 305-310.

Zoltai, S.C. 1972. Palsas and peat plateaus in central Manitoba and Saskatchewan. Canadian Journal of Forest Research **2:** 291-302.

Zoltai, S.C. 1988. Wetland environments and classification. *In* Wetlands of Canada. Ecological Land Classification series, No. 24. *Edited by* National

Wetlands Working Group. Polyscience Publications Inc., Montreal. pp. 1-23.

Zoltai, S.C. 1995. Permafrost distribution in peatlands of west-central Canada during the Holocene warm period 6000 years B.P. Géographie Physique et Quaternaire **49:** 45-54.

Zoltai, S.C. and Tarnocai, C. 1971. Properties of a wooded palsa in northern Manitoba. Arctic and Alpine Research **3:** 115-129.

CHAPTER 3:

PLANT COMMUNITY CHANGE DUE TO LOCALIZED PERMAFROST DYNAMICS IN BOREAL WESTERN CANADIAN BOGS

3.1 INTRODUCTION

Permafrost is an important part of Canada's north, as Continuous and Discontinuous Permafrost Zones cover about half the country's landmass (Heginbottom 1995). Permafrost is a ground temperature phenomenon, defined as earth materials that remain below 0°C for two or more years (Harris *et al.* 1988). As such, it is sensitive to environmental changes that affect ground temperature at the microclimate to regional climate scales (Williams and Smith 1989), especially at the climatic limits of its occurrence. Thus factors such as disturbance (that affects the local microclimatic conditions) and long term regional climatic change determine whether it is aggrading, degrading or is in equilibrium with its environment. Interest in permafrost at its climatic limit is thus increasing due to its value as a climate change indicator (Washburn 1980; Sollid and Sorbel 1998), as well as the importance of determining the ecological effects of its ongoing degradation (Woo *et al.* 1994).

In the Discontinuous Permafrost Zone, permafrost occurs most commonly in treed boreal and subarctic peatlands, that can be divided into two types based on morphology (Brown 1968): large expansive peat plateaus (completely underlain by permafrost), and small restricted landforms of isolated permafrost in largely unfrozen peatlands (localized permafrost peatlands, Chapter 2). The distribution of these two morphologies follows climate (Vitt *et al.* 1994; Halsey *et al.* 1997; Chapter 2) and localized permafrost peatlands are concentrated at the southern limit of permafrost in continental western Canada (Alberta, Saskatchewan, and Manitoba). Localized permafrost in peatlands is degrading throughout its range (Vitt *et al.* 1994; Vitt *et al.* 2000), leaving areas of localized

permafrost collapse (internal lawns) in peatlands, and has completely disappeared at some locations near its southern limit (Chapter 2).

Peatland plant communities have been moderately well studied in western Canada. General plant communities were described in early studies (Lewis and Dowding 1926; Lewis *et al.* 1928; Moss 1953). More recent work has focussed on patterns of vegetation relative to environmental gradients across different peatland types (Jeglum 1973; Kenkel 1987; Vitt and Chee 1990), and within peatland types for fens (Vitt *et al.* 1975 - poor fens; Slack *et al.* 1980 – extreme-rich fens; Chee and Vitt 1990 – moderate-rich fens), bogs (Belland and Vitt 1995) and peat plateaus (Horton *et al.* 1979). Although the bryophytes of permafrost peatlands have been included in some of these studies (notably Belland and Vitt (1995) and Vitt *et al.* (1995)), and the vegetation has been roughly described (Vitt *et al.* 1994), the plant communities of localized permafrost peatlands have not been investigated in detail (with the exception of a single frost mound (treed palsa) described by Zoltai and Tarnocai (1971)). Vegetation change in localized permafrost bogs and the ecological conditions it indicates must be characterized if the impact of ongoing permafrost degradation, that may accelerate with predicted climate change, is to be fully understood.

3.1.1 Objectives

The objective of this study is to determine patterns of vegetation change in western Canadian continental bogs affected by localized permafrost dynamics. Specifically, I address two questions; 1) How do plant communities and diversity in continental bogs respond to localized permafrost formation and melt as determined through comparison of plant communities between continental bogs, frost mounds and internal lawns? 2) How do plant communities vary within internal lawns, and how do community and diversity patterns relate to peatland development following permafrost melt?

3.1.2 Study region and peatland sites

Localized permafrost peatlands occur in a wide belt across boreal Alberta, Saskatchewan and Manitoba, and cover 17,505 km^2 (Chapter 2). This area largely falls within Zoltai *et al.*'s (1988) Continental High Boreal Wetland Region and is characterized by low precipitation (relative to coastal boreal wetland regions) and cold winters, where localized permafrost peatlands are a characteristic wetland type (referred to as palsa bogs by Zoltai *et al.* (1988)). To determine the effects of permafrost dynamics on vascular plant and bryophyte vegetation, three localized permafrost bogs were selected for study in each of Alberta, Saskatchewan and Manitoba from aerial photography of the whole region. These were chosen to have distinct frost mounds and internal lawns, reasonable accessibility, and to span the longitude of the region. These bogs occur where localized permafrost landforms are the dominant permafrost feature (peat plateaus occur only rarely nearby (Chapter 2)), near the southern border of the localized permafrost peatland region (Fig. 3-1) and the southernmost limit of permafrost. Regional climate and the degree of degradation are comparable for all three peatlands (Table 3-1).

3.2 METHODS

3.2.1 Plant community surveys

To determine the effect of permafrost aggradation and degradation on bog plant communities three distinct landforms were surveyed, and included continental bog (the background vegetation matrix in which localized permafrost landforms occur), frost mounds, and internal lawns (Fig. 3-2). The vegetation of ten landforms of each type was assessed in each peatland (with the exception of frost mounds at the Patuanak, SK peatland, where only 9 were found) for a total of 89 landform relevés. Bog vegetation was evaluated by locating random coordinate points from a grid overlain onto large-scale aerial photographs of each site. The general area of each point was located on the ground, and a 5 x 5 m plot placed within a representative area of vegetation. Percent cover of all

vascular plant and bryophyte species, and all lichens over 1% cover, was estimated visually within each plot. Cover data were supplemented by a search for new species within a 25 m radius until no new species were found. Species that occurred outside relevés were assigned a cover value of 0.05% for abundance analyses. Frost mounds and internal lawns were randomly selected from the total accessible population of landforms in each site. Frost mounds were surveyed by the same technique used to survey bog plant communities. Internal lawns have the most variable vegetation and surface wetness conditions of the three landform types, due to the effects of time-transgressive degradation and subsequent peatland development, and could not be accurately sampled using 5 x 5 m plots. Instead, abundance values were estimated for each entire landform. Estimates of abundance were facilitated by the open, largely treeless nature of internal lawns. Internal lawn edges represent a transition between affected and unaffected bog, as pre-existing localized permafrost lenses thin out at their margins (Zoltai 1972), resulting in decreased disturbance when permafrost thaws. A one-meter margin around the inside border of each internal lawn was therefore excluded from surveys to ensure only vegetation affected by permafrost melt was included. Water samples from pools or shallow, excavated pits in each bog and internal lawn relevé was collected in acid-washed polyethylene bottles. Samples were refrigerated and the pH and conductivity (corrected for pH following Sjörs 1952) of each sample were determined in the lab.

To determine the spatial variability in vegetation resulting from post-melt peatland development, an additional five internal lawns were randomly chosen in each peatland for finer-scale survey. Internal lawns are typically oblong or irregular in shape (Fig. 3-2), and degrade along 'melting fronts' following the initiation of melt, creating a newly collapsed area and an older area. To capture the range of conditions along this temporal/wetness gradient, a central transect was placed along the longest axis of each internal lawn. This transect was divided into 10 equal lengths, and a two-meter diameter round quadrat was

randomly placed within each length (10 quadrats per internal lawn, 50 quadrats per peatland, 150 quadrats total). Within each quadrat cover values of all vascular plants and bryophytes, and lichens that had cover values greater than one percent, were visually estimated. The modal height of the peat surface above the water table and microrelief were measured for each quadrat. Microrelief was estimated by measuring the height between the highest hummock top and the lowest hollow bottom within each quadrat.

In all surveys, all vascular plants and bryophytes were identified to species. True mosses and *Sphagnum* are treated separately, and 'mosses' refer to non-*Sphagnum* mosses hereafter. Species names follow Moss (1983) for vascular plants, Ireland *et al.* (1987) for mosses and *Sphagnum*, Stotler and Crandall-Stotler (1977) for hepatics, and Esslinger and Egan (1995) for lichens.

3.2.2 Data analysis

Non-metric multidimensional scaling (NMDS) was used to compare vegetation from bog, frost mound and internal lawn relevés. NMDS is a non-parametric dimension reduction technique that works without assumption of linear or unimodal response, and escapes many of the distortions of eigenvector techniques (Kenkel and Orlóci 1987; Minchin 1987; Legendre and Legendre 1998). Sorensen (Bray-Curtis) distance was used as a general measure of ecological similarity (Faith *et al.* 1987) for all NMDS ordinations. To thoroughly explore the effects of permafrost dynamics on total bog vegetation as well as on the vascular plant and bryophyte components, four analyses were run using different data subsets: 1) abundance data for total vegetation including coverages for lichen species that had >1% cover (*Cladina mitis*, *C. rangiferina*, *C. stellaris*) and coverages of bare peat, 2) vascular plant and bryophyte presence/absence, 3) vascular plant presence/absence, and 4) bryophyte presence/absence. Differences in pH and conductivity between bog and internal lawn surface waters were determined by Mann-Whitney U tests (Zar 1999).

Summary statistics and tests for pH were conducted on hydrogen ion concentrations, and reported as pH.

In order to decrease the effect of the few *Sphagnum* species that dominated each of the small quadrats (and thereby increase the sensitivity of analyses to patterns from less common species) abundance values in the quadrat dataset were square-root transformed. The 150 internal lawn quadrats were then classified using Sorensen distance between quadrats and flexible beta clustering (beta = -0.25) (Legendre and Legendre 1998). Groups were named by their dominant vegetation (*Sphagnum* species). Transformed abundance data from these quadrats were ordinated by NMDS. All multivariate analyses were implemented in PC-ORD (McCune and Mefford 1999).

Alpha, beta and gamma diversity were assessed following the diversity concepts of Whittaker (1970). Alpha diversity was calculated as the mean number of species (richness) in bogs, frost mounds, or internal lawns from the relevé data, or the mean number of species in each vegetation group for the internal lawn quadrat data. Beta diversity was calculated for both relevé and quadrat data as the ratio of total number of species in each dataset to the mean richness across all sample units (all 89 relevés, or all 150 quadrats). Gamma diversity was defined as the total species richness from all surveys in all three peatlands (the landscape diversity of localized permafrost bogs). The equality of mean alpha diversity values between internal lawn quadrat groups was determined by Kruskal-Wallis H tests.

3.3 RESULTS

3.3.1 Community/floristic ordinations, vegetation patterns, and water chemistry

Ordination of abundance data for the total vegetation (including lichen and bare peat cover) did not have a substantially lower stress value for solutions

beyond two dimensions: final 2-D stress was 7.6. Landform groups are clearly separated, with bog relevés intermediate on the diagram, and frost mounds and internal lawns clearly separated at the ends of the first NMDS axis (Fig. 3-3A). Between-peatland differences are greatest in the frost mound and internal lawn vegetation, evident in the higher degree of closeness and clumping of localized permafrost landform data points from the same peatland compared to the more freely intergrading bog vegetation on the diagram. Broad vegetation patterns between landforms are shown by plotting tree cover values (*Picea mariana*) and ground cover values (ground cover by *Sphagnum* spp., feathermosses (*Pleurozium schreberi*, *Hylocomium splendens*, and *Ptilium crista-castrensis*) and lichens) onto the ordination space (Fig. 3-3B through E). Landform types differed markedly in tree cover (Fig. 3-3B), and were nearly always bryophyte-dominated in ground cover (ranging from *Sphagnum* to feathermoss dominance). Bog vegetation (unaffected by permafrost) was characterized by open *Picea mariana* and was always *Sphagnum*-dominated. Frost mounds had *Picea* cover greater than that of bog relevés (more than double on average (Fig. 3-3B), and often resulted in closed canopies), and had ground cover dominated by feathermosses (except for seven frost mounds in the Moose Lake, MB peatland that were dominated by lichens of the genus *Cladina* - Fig. 3-3C and 3-3E). Internal lawn tree cover was less than one percent on average and did not exceed three percent. Sparse tree cover present was from stray collapse survivors or newly established spruce on older, drier surfaces. Ground cover in internal lawns was strongly dominated by *Sphagnum* (Fig. 3-3D), with much reduced cover by other mosses and a nearly complete exclusion of lichen (Fig. 3-3E). Two-thirds of the internal lawns had *S. fuscum* cover greater than 50%, and mean cover of *S. fuscum* in all internal lawns was 63.4%.

Surface water pH in bogs (mean = 3.65) and internal lawns (mean = 4.02) ranged between 3.08 and 4.49, and were statistically different ($P < 0.001$). Surface water corrected conductivity (bog mean = 15.0 µS/cm; internal lawn mean = 52.2 µS/cm) was also significantly higher after permafrost collapse ($P <$

0.001). pH and conductivity are shown plotted within the vegetation ordination space in Figure 3-4.

Ordination of relevés based only on the presence/absence of species using both vascular plant and bryophyte species also shows distinct separation of frost mounds from internal lawns, though some overlap occurs between bog and internal lawn relevés (Fig. 3-5A). Between-peatland differences (within landform types) are not as clearly expressed in the floristic data as in the abundance data (compare Fig. 3-3A and 3-5A), and relevé points from the different peatland sites overlap more freely when only presence/absence is used. Separate floristic analyses of the vascular plant and bryophyte vegetation components by NMDS show that much of the landform separation and general pattern in the total vegetation data comes from the bryophyte component of the data (Fig. 3-5C) and less from the vascular plant component (Fig. 3-5B). Vascular plant species ordination had a final stress of 16.59, and bryophyte species had a final stress of 22.06; both had the best solution in two dimensions. Both ordinations show a distinct position of frost mound points from bog and internal lawn points in the ordination space. However, the vascular plant analysis shows strong floristic overlap of *Sphagnum*-dominated bog and internal lawn relevés.

3.3.2 Diversity

Seventy-three vascular plant and bryophyte species were encountered in the three localized permafrost bogs; 20 vascular plants, 26 true mosses, 11 *Sphagnum* mosses, and 16 hepatics (complete list provided in Appendix 1 and 2). Comparison of species diversity among landforms reveals that mean alpha diversity is similar in bogs and internal lawns, and lower in frost mounds (decrease of 31% from bog, Table 3-2). This decrease due to permafrost aggradation is largely due to reduction in the number of vascular plant, *Sphagnum* and hepatic species, though moss diversity increased and was highest in frost mounds. Vascular plant diversity is nearly double in internal

lawns relative to frost mounds, due to presence of common bog species in addition to *Betula pumila*, *Scheuchzeria palustris* and species of *Carex* (plants common in poor fens (Vitt *et al.* 1975) and absent from bog relevés). Internal lawn vascular plant diversity was higher than that of the bog matrix. *Sphagnum* diversity was much higher in internal lawns compared to frost mounds, and also exceeded that of the bog relevés due to the introduction of species that were either rare or absent from the bogs (*Sphagnum jensenii, S. obtusum, and S. lindbergii*). Hepatic diversity was highest in *Sphagnum*-dominated bog and internal lawn relevés, though cover values were greatest in frost mounds due to the presence of large mats of *Mylia anomala*. Moss diversity was lowest in internal lawns (Table 3-2). Beta diversity was greatest for true mosses and hepatics, with lower values for *Sphagnum* and lowest values for vascular plants (Table 3-2).

3.3.3 Internal lawn vegetation

Vegetation from the intra-internal lawn surveys was divided into six groups by cluster analysis (Fig. 3-6), and named for their dominant (*Sphagnum*) species. Nearly two-thirds of the quadrats were strongly *Sphagnum fuscum* dominated (greater than 90% cover, on average). Another 20 quadrats included *S. fuscum* as a dominant species (> 50%), but also included high cover of *S. magellanicum*, *S. russowii*, and *S. angustifolium* (named mixed *S. fuscum*). Twenty quadrats were dominated by *S. angustifolium*, though these also included up to 20% coverage by *S. riparium*. Six quadrats were *S. riparium* dominated, three quadrats were *S. russowii* dominated, and a single quadrat had 98% *S. jensenii* cover. NMDS ordination of the internal lawn quadrats supports the groups from the cluster analysis (Fig. 3-7), and had a final stress of 13.8. The 98 *S. fuscum* quadrats are closely clustered on the right side of the diagram, whereas the remaining quadrats show greater compositional variability on the left of the diagram.

Ordering internal lawn plant community groups by increasing height above water table shows that microrelief reached its greatest value in mixed *S. fuscum* communities, with a slight decrease when *S. fuscum* comes to dominate (Fig. 3-8). Mean alpha diversity of all species does not significantly change between groups ($P = 0.60$). When separated into vascular plant and bryophyte components, opposite trends in species richness are evident; vascular plant richness slightly increases with height above water table ($P < 0.001$), while bryophyte richness does not significantly change ($P = 0.20$). Variability in height above water table and mean alpha diversity (total, vascular plant and bryophyte) decreases along the vegetation sequence (Fig. 3-8).

3.4 DISCUSSION

Gradient analyses across North American peatland types show that peatland vegetation patterns are generally determined by surface water chemistry and wetness gradients (Kenkel 1987; Glaser *et al.* 1990; Vitt and Chee 1990; Jeglum and He 1995). In western Canadian continental bogs, water chemistry gradients are truncated (relative to rich fens) and other environmental factors such as shade and dryness have a greater effect on vegetation (Belland and Vitt 1995). In contrast to permafrost that occurs in dry Continuous Zone bedrock or Discontinuous Zone upland soils, the abundance of water in saturated subsurface peat leads to the elevation of permafrost-underlain surfaces above water tables due to the volumetric expansion and buoyancy of ice (Zoltai 1972). Soil conditions on frost mounds become free from water table influence, and depth to the permafrost on frost mounds is typically around 60 cm but can be over 100 cm (Zoltai and Tarnocai 1971; Zoltai 1972). *Picea mariana* has been shown to respond strongly to decreased peatland water table (Dang and Lieffers 1989; Lieffers and MacDonald 1990), and increased tree vigor results in a more shaded ground cover (Fig 3-3B). Degradation of localized permafrost results in collapse of the frost mound surface to below that of the surrounding bog, creating open conditions that are clearly evident on aerial photographs when trees are

drowned (Vitt *et al.* 1994). Localized permafrost aggradation and degradation at the southern limit of permafrost thus has a great influence on peatland vegetation, as frost mounds and internal lawns represent the driest/shadiest and wettest/most open conditions that occur in Canadian continental bogs.

3.4.1 Community/floristic ordinations and vegetation patterns

The clear separation of landform relevés on the total vegetation abundance data ordinations (Fig. 3-3A) shows that the landform groups are well supported by the vegetation data, and that localized permafrost aggradation and degradation results in landforms with distinct plant communities. Separation is complete between frost mounds and internal lawn relevés on both total species abundance and floristic ordination diagrams (Fig. 3-3A and 3-5A) clearly showing that non-wetland conditions can be created by permafrost aggradation, and the unique, wet conditions created by permafrost melt. The position of frost mound relevés is most distinct in the ordinations, due to their unique vegetation and low diversity. Change in tree cover between landforms is impressive (Fig. 3-3B), and of importance in its effect on peatland habitat (*P. mariana* is the only source of large physiognomic structure in bogs), the influence on understory vegetation (Camill 1999a, Belland and Vitt 1995), and potential changes in carbon sequestration due to increased tree vigor. The dense tree cover, feathermoss/lichen groundcover and isolation from peatland water tables make frost mound plant communities more similar to boreal upland black spruce ecosystems than wetlands (*cf.* LaRoi and Stringer 1976). Permafrost degradation in boreal peatlands can proceed quickly once initiated (Thie 1974; Engelfield 1994), thus the large community change that occurs when permafrost degrades (evident in distance and separation between frost mound and internal lawn points in Fig. 3-3A and 3-5A) is very fast. Since linear collapse rates are faster in warmer regional climates (Camill and Clarke 1998), these large community changes may occur even more rapidly with the 5°C increase in mean annual temperature predicted for the region over the next century (Boer *et al.* 2000).

In general, plant community change in boreal forest ecosystems (at temporal scales from decades to centuries) is largely under control of disturbance from fire (Johnson 1992; Payette 1992). Although fire also occurs frequently in boreal peatlands (Wein 1983), macrofossil evidence shows that bogs recover quickly from fire with tree cover and *Sphagnum* ground cover returning quickly to pre-fire conditions (Kuhry 1994). Permafrost degradation, on the other hand, results in longer, more pronounced changes in bog vegetation (Zoltai 1993; Camill 1999b; Chapter 4). Frost mound collapse after permafrost melt is likely the greatest disturbance that occurs in boreal and subarctic ombrogenous peatlands. This, perhaps, is greatest when melt is initiated by fire that results in loss of surface peat and therefore greater collapse relative to water table upon melt). The magnitude of this disturbance is evident in the significant increases in pH and conductivity between bogs and internal lawns, and suggests that internal lawns can collapse to the degree that they become geogenous (are in contact with minerotrophic ground water), and are in fact poor fens. It is likely that minerotrophic conditions occur in newly melted landforms, and that ombrogenous conditions return after a given amount of peat accumulates. This is further supported by the common occurrence of *Sphagnum jensenii* and *Cladopodiella fluitans* in internal lawns, species that Vitt and Belland (1995) recommend as poor fen indicators.

Between-peatland differences are clearly evident in the abundance data and less distinct in the floristic data, and show that differences between peatlands are more strongly expressed in changes in the cover of species that occur in all three sites, rather than in the addition or removal of species between peatlands. Between-peatland differences in frost mound plant communities are related to the degree of environmental change caused by permafrost aggradation. For example, Zoltai and Tarnocai (1971) found that the densest and tallest tree growth, that was correlated to ground vegetation cover by mosses and lichens, was associated with the thickest permafrost lenses.

Differences in the magnitude of permafrost aggradation between peatlands is determined by past conditions, including site-specific hydrology and plant communities (that affected surface thermal balances when permafrost formed), and regional climate patterns during the Little Ice Age (that may have been substantially different from present patterns). Differences in internal lawn vegetation between peatlands are closely related to the permafrost conditions expressed in the frost mound vegetation data, and the amount of time passed since degradation (increased time for peat accumulation and succession). Since permafrost aggradation also affects the composition of the peat (Zoltai 1993) and the rate at which it vertically accumulates relative to undisturbed peat accumulation in the surrounding bog (Turetsky *et al.* 2000), differences in permafrost conditions determine the degree of landform collapse when permafrost melts. Between-peatland differences in frost mound and internal lawn plant communities are attributable to differing permafrost conditions, as well as possible asynchronous degradation.

3.4.2 Diversity

Continental bogs are floristically simple, consistent ecosystems with the lowest bryophyte diversity of all peatland types (Vitt *et al.* 1995) and low vascular plant diversity compared to coastal bogs (Glaser 1992). Bryophyte diversity in continental bogs is strongly associated with microhabitat heterogeneity (Vitt *et al.* 1995). Frost mounds lack the dryness gradient present along the peatland hummock-hollow sequence, evident in the decreased mean alpha diversity values in permafrost compared to bog relevés. However, the abundance of shaded, cool forest floor and tree base microhabitats results in increased forest floor moss diversity on frost mounds (species of *Ceratodon*, *Dicranum*, and feathermosses (*Ptilium* and *Hylocomium*) that are more uncommon in bogs). Internal lawn mean alpha diversity (particularly *Sphagnum* diversity) is greater than that of frost mounds due to the presence of the peatland dryness gradient. In internal lawns, this gradient is lengthened due to the presence of very wet, nearly aquatic conditions in newly collapsed areas and the presence of carpet

vegetation. Moss diversity, however, is very low in internal lawns. Since the availability of microhabitats in peatlands is strongly affected by the presence of trees (of the nine peatland microhabitats named by Vitt *et al.* (1995), four are associated with tree bases), moss diversity will likely rebound following tree establishment and growth.

3.4.3 Internal lawn vegetation

Peat accumulation rates in internal lawns have been shown to exceed those in non-permafrost affected bogs (Turetsky *et al.* 2000), a phenomenon also observed in more northern collapse scars within peat plateaus (Camill 1999b). Resultant accelerated changes in internal lawn surface height above water table drives post-melt plant community succession quickly (Zoltai 1993, Camill 1999b, Chapter 4). The strong groups recognized by cluster analysis reflect both the *Sphagnum*-dominated nature of internal lawn vegetation in bogs, as well as the well defined niche space of *Sphagnum* along the wetness gradient (Horton *et al.* 1979; Vitt and Slack 1984). The large number of quadrats dominated by dry-adapted *Sphagnum fuscum* is indicative of accelerated temporal change in internal lawns as peat quickly accumulates (also supported by the abundance of *S. fuscum* in internal lawns from landform relevés). Organization of these groups by their mean height above water table reflects the developmental series from wet to dry taking place in internal lawns following permafrost collapse. These mean height above water table values are supported by those reported from autecological studies of *Sphagnum* species' tolerances and optima relative to peatland water tables (Gignac *et al.* 1991; see Chapter 4). Microrelief increases along this series, as newly collapsed surfaces have even microtopography due to very wet conditions and the occurrence of wet-adapted sphagna occurring in carpets (*S. jensenii*) and lawns (*S. riparium* and *S. angustifolium*). Further peatland development and establishment of hummock-forming species at higher levels above the water table brings increased microtopography. The slight decrease in microrelief when vegetation becomes strongly dominated by *S.*

fuscum represents the loss of hollow microhabitat within the area captured by quadrats.

Most diversity change across the sequence is captured in the beta diversity values, as mean alpha diversity does not change significantly across the sequence. Species turnover is greatest in bryophytes regardless of non-significant mean alpha diversity changes, largely due to the localized sensitivity of bryophytes to microhabitat wetness compared to rooting vascular plants. Thus the greatest diversity in any internal lawn occurs when this dryness gradient is maximized, i.e. melt sites that have both recently degraded and older, drier surfaces. This time-transgressive pattern of permafrost melt within individual internal lawns is common across the study region and is most evident in features with recently degraded surfaces. The period of high variability in mean alpha plant diversity and dryness following permafrost melt and initial peatland development is followed by reduced variability as surfaces converge on *S. fuscum*-dominated vegetation. The eventual establishment of trees in internal lawns will re-introduce associated microhabitat conditions and likely increase moss diversity towards bog values (Table 3-2).

3.4.4 Landscape implications

The mean alpha diversity of frost mounds and internal lawns are lower than or equivalent to that of the bog matrix that surrounds them. However, the total number of species increases by 49% when additional species present in frost mounds and internal lawns are added to the list of species found only in the bog surveys (Table 3-2). Vitt *et al.* (1995) summarized bryophyte gamma diversity by peatland type and noted that bryophyte species richness is 19% higher in peat plateaus (with collapse scars) than in bogs. The total bryophyte gamma diversity of the three localized permafrost bogs surveyed in this study (54 species) is more comparable to diversity in peat plateaus (44 species; Vitt *et al.* 1995) than continental bogs (38 species, this study; 37 species Vitt *et al.* 1995). Permafrost dynamics, whether they result in frost mounds and/or internal lawns

or peat plateaus with collapse scars, increase species diversity in similar ways, by the creation of habitat conditions absent from bogs. The bryophyte gamma diversity of localized permafrost bogs is as high as pooled gamma diversity from both continental bogs and peat plateaus, and second only to extreme-rich fens in western Canada (Vitt *et al.* 1995). Thus, localized permafrost bogs are previously undescribed centres of bryophyte diversity in the mosaic of peatland types in the expansive peatlands of western Canada.

Table 3-1. Climate and physiography of three localized permafrost bogs studied. Landform areas were calculated from mapped and digitized small scale aerial photography taken between 1987 and 1995 in Arc/Info. Climate data is taken from 1951-1980 climate normals (Environment Canada 1982) from the nearest permanent climate station to each peatland except for mean annual temperature at Patuanak, that follows interpolated mean annual temperatures corrected for elevation from Vitt *et al.* (1994), due to lack of temperature data in the climate normals.

		Anzac Bog, AB	Patuanak Bog, SK	Moose Lake Bog, MB
Climate	Mean annual temperature (°C)	-0.4	-1.0	-1.2
	Mean annual precipitation (mm)	471.9	443.9	495.6
Peatland	Bog form†	flat bog	plateau bog (islands)	plateau bog (islands)
	Total bog area (km^2)	6.97	1.33	4.07
	Total frost mound and internal lawn area (km^2)	0.11	0.09	0.17
	Extent of degradation (% by area)	60.3	65.5	53.2

†after Zoltai *et al.* (1988).

Table 3-2. Summary of mean alpha (species richness) and beta diversity from bog, frost mound, and internal lawn surveys, from three localized permafrost bogs in continental western Canada.

		Bog	Frost Mound	Internal Lawn	All Landforms	**Beta Diversity**
Mean Alpha Diversity	Total	22.6	15.6	22.1	20.2	**3.66**
	Vascular plant	8.3	5.4	9.8	7.9	**2.54**
	Bryophytes	14.3	10.2	12.3	12.8	**4.22**
	Sphagnum	4.1	1.1	5.9	3.8	**2.93**
	Mosses	5.3	6.3	2.6	4.7	**5.51**
	Hepatics	4.9	2.8	3.8	3.8	**4.44**
Total Species Richness	All species	49	45	56	73	

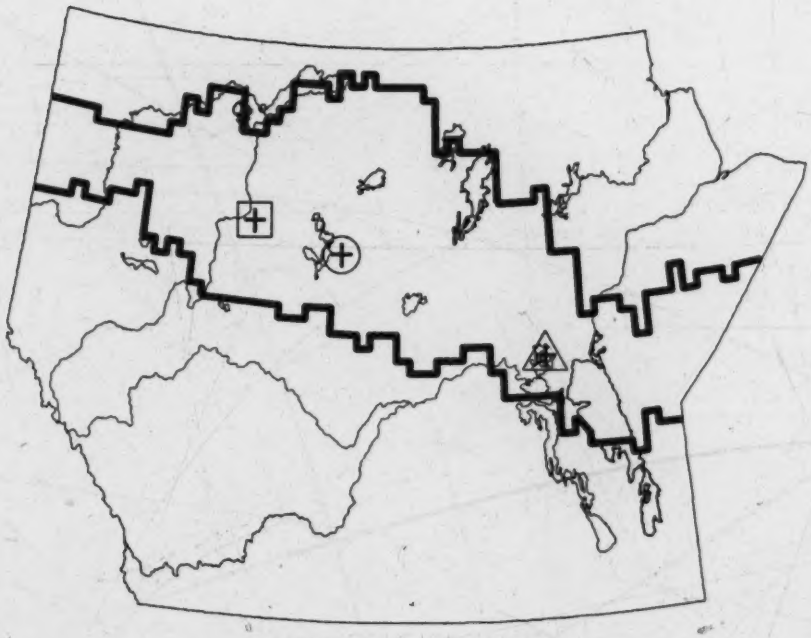


Fig. 3-1. Continental western Canada (Alberta, Saskatchewan, and Manitoba) with the outline of the localized permafrost peatland region and location of study sites; Anzac, AB (square), Patuanak, SK (circle), and Moose Lake, MB (triangle).

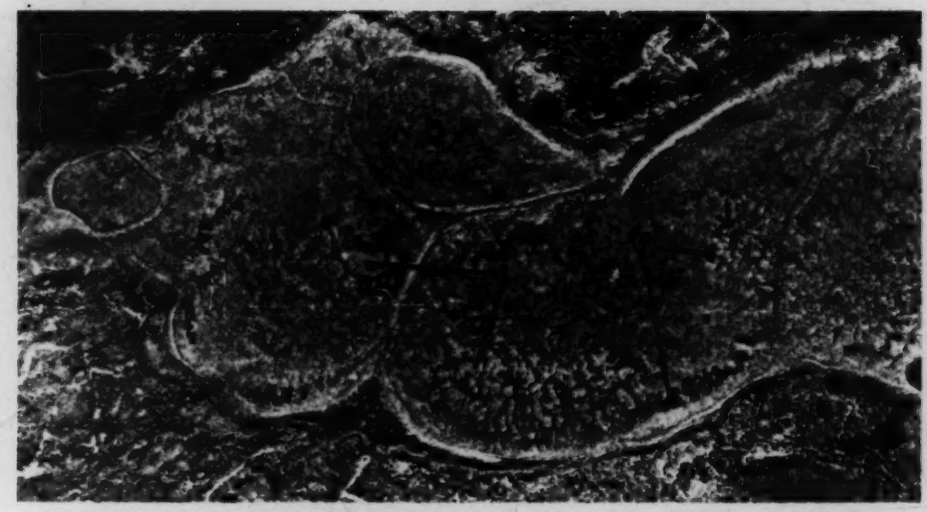


Fig. 3-2. Aerial photograph of the Moose Lake, MB localized permafrost bog. Treed frost mounds (f) and internal lawns (i) occur within the continental bog (b) matrix.

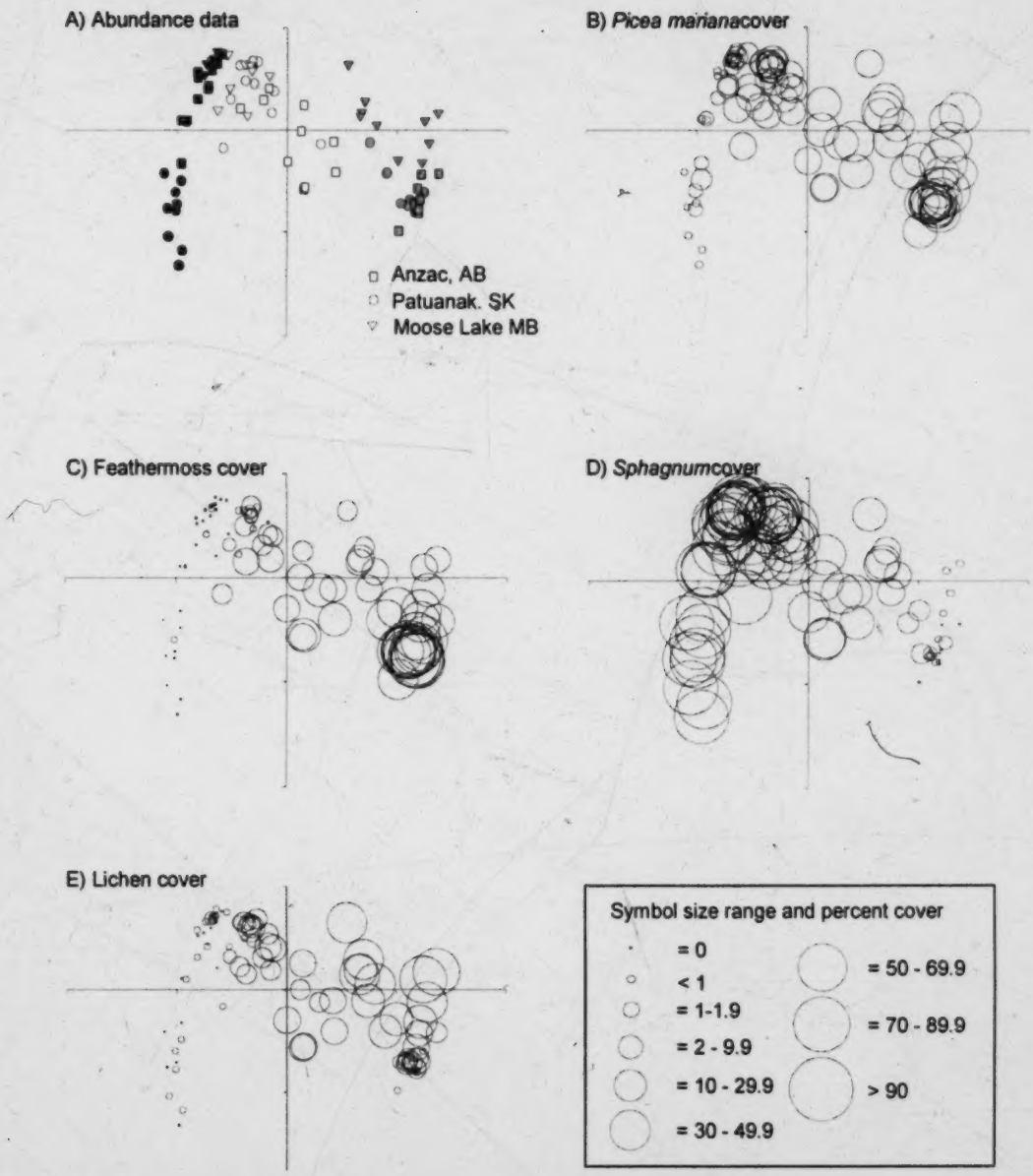


Fig. 3-3. NMDS ordination of total species abundance data from bog (white symbols), frost mound (light grey symbols) and internal lawn (dark grey symbols) landform relevés. Tree cover by *Picea mariana*, and ground cover by feathermosses, *Sphagnum* spp., and lichen in each relevé are shown on the ordination space.

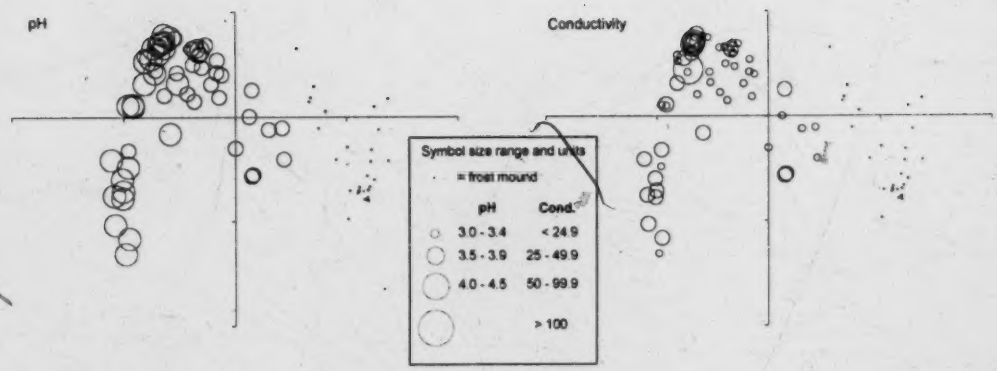


Fig. 3-4. Surface water pH and corrected conductivity from bog and internal lawn relevés plotted on total abundance data NMDS space. Dots are frost mound relevés (frozen peat without surface water).

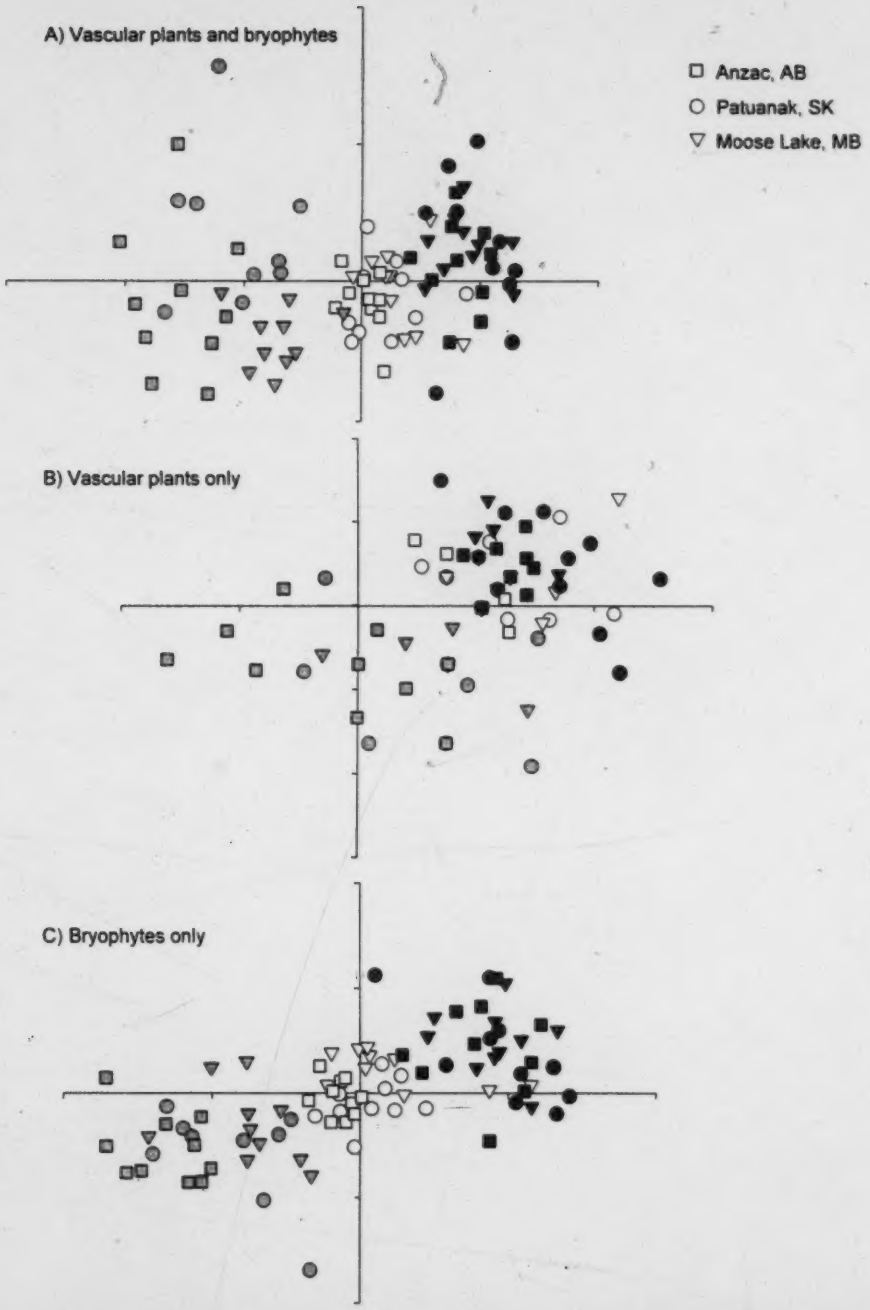


Fig. 3-5. NMDS ordinations of presence/absence data for vascular plants and bryophytes (A), vascular plants only (B) and bryophytes only (C). White symbols = continental bog, light grey symbols = internal lawn, and dark grey symbols = frost mound relevés.

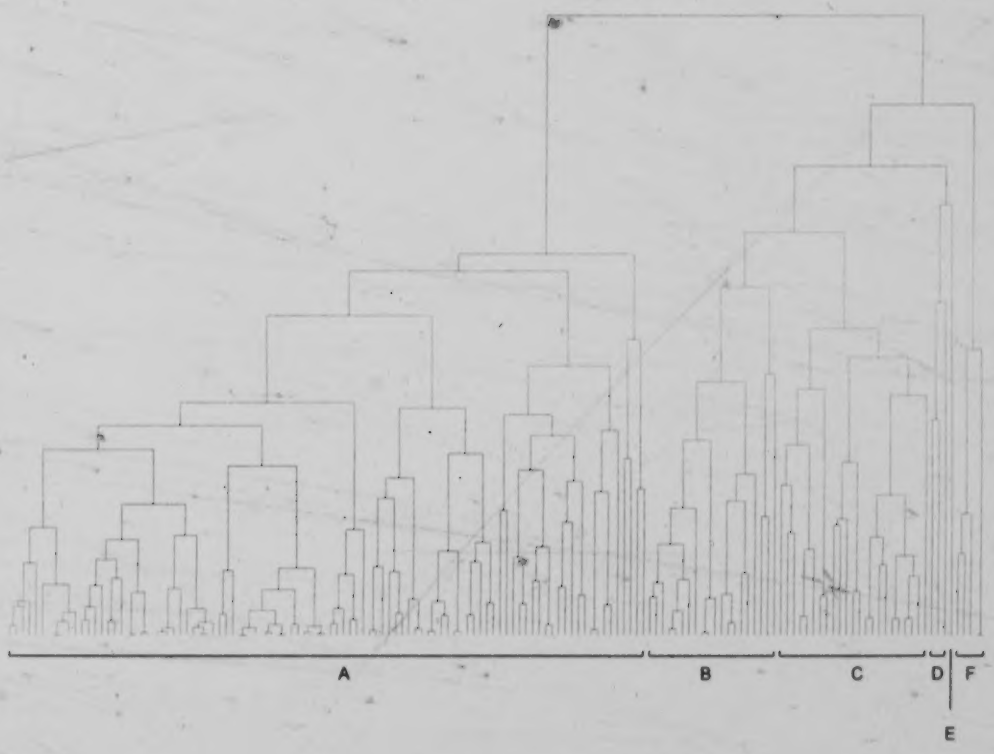


Fig. 3-6. Dendrogram of the flexible Beta (β = 0.25) cluster analysis (Sorensen distance) of 150 internal lawn quadrats following square-root transformation of abundance data. The six strongest groups are shown and correspond to dominance by *Sphagnum fuscum* (A), mixed *S. fuscum* (B), *S. angustifolium* (C), *S. russowii* (D), *S. jensenii* (E) and *S. riparium* (F).

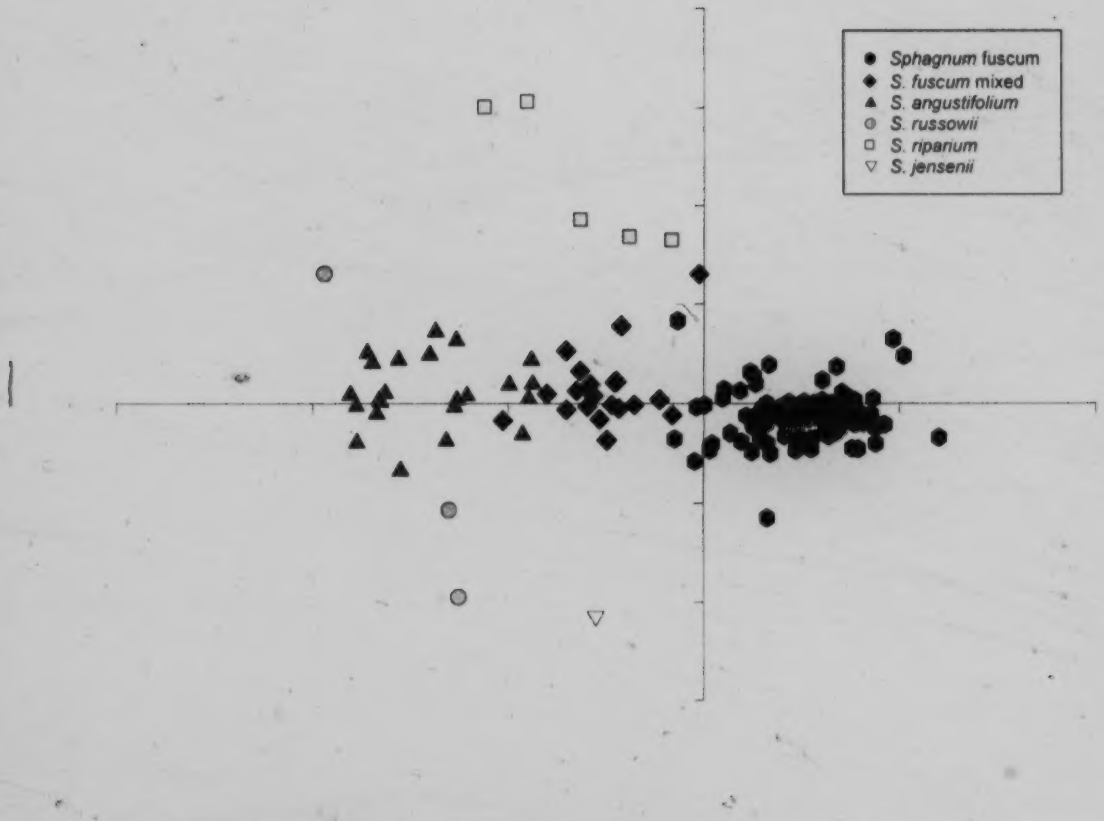
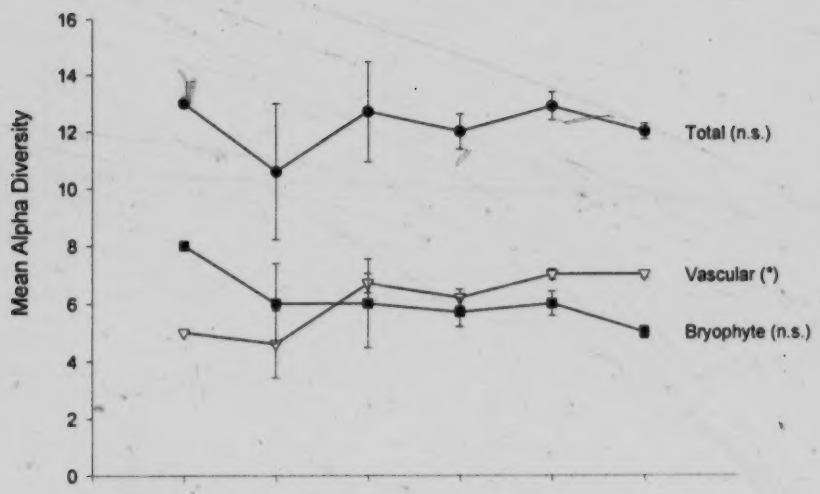


Fig. 3-7. NMDS ordination of 150 internal lawn quadrats, using square-root transformed cover data.



		jensenii *riparium*	*russowii*	*fuscum* mixed *angustifolium*		*fuscum*
Mean height above water table (cm) (standard deviation)	2	17.6 (3.36)	18.0 (4.04)	24.2 (1.59)	25.1 (1.43)	25.1 (0.92)
Microrelief (cm) (standard deviation)	13	19.2 (3.10)	18.3 (4.70)	18.3 (1.62)	22.7 (2.10)	21.3 (0.78)

Fig. 3-8. Patterns of mean alpha diversity and microrelief among vegetation groups from 150 internal lawn quadrats, shown in increasing order of height above water table. Error bars show standard deviations. The *Sphagnum jensenii* group has only one quadrat. Non-significant (n.s.) and significant (* - P <.05) results following Kruskal-Wallis H tests are indicated.

3.5 LITERATURE CITED

Belland, R.J. and Vitt, D.H. 1995. Bryophyte vegetation patterns along environmental gradients in continental bogs. Écoscience **2:** 395-407.

Brown, R.J.E. 1968. Occurrence of permafrost in Canadian peatlands. Proceedings of the Third International Peat Congress, Quebec. pp. 174-181.

Camill, P. 1999a. Patterns of boreal permafrost peatland vegetation across environmental gradients sensitive to climate warming. Canadian Journal of Botany **77:** 721-733.

Camill, P. 1999b. Peat accumulation and succession following permafrost thaw in boreal peatlands of Manitoba, Canada. Écoscience **6:** 592-602.

Camill, P. and Clark, J.S. 1998. Climate change disequilibrium of boreal permafrost peatlands caused by local processes. The American Naturalist **151:** 207-222.

Chee, W-L. and Vitt, D.H. 1989. The vegetation, surface water chemistry and peat chemistry of moderate-rich fens in central Alberta, Canada. Wetlands **9:** 227-261.

Dang, Q.L. and Lieffers, V.J. 1989. Assessment of patterns of response of tree ring growth of black spruce following peatland drainage. Canadian Journal of Forest Research **19:** 924-929.

Engelfield, P.G.C. 1994. Rate of permafrost degradation in peatlands. M.Sc. Thesis. University of Alberta, Edmonton, Alberta. 33 pp.

Environment Canada. 1982. Canadian Climate Normals 1951-1980. Environment Canada. Ottawa, Canada.

Esslinger, T.L. and Egan, R.S. 1995. A sixth checklist of the lichen-forming, lichenicolous, and allied fungi of the continental United States and Canada. The Bryologist **98:** 467-549.

Faith, D.P., Minchin, P.R., and Belbin, L. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio **69:** 57-68.

Gignac, L.D., Vitt, D.H., Zoltai, S.C., and Bayley, S.E. 1991. Bryophyte response surfaces along climatic, chemical and physical gradients in mires of western Canada. The Bryologist **93:** 7-22.

Glaser, P.H. 1992. Raised bogs in eastern North America - regional controls for species richness and floristic assemblages. Journal of Ecology **80:** 535-554.

Glaser, P.H., Janssens, J.A., and Siegel, D.I. 1990. The response of vegetation to chemical and hydrological gradients in the Lost River peatland, northern Minnesota. Journal of Ecology **78:** 1021-1048.

Halsey, L.A., Vitt, D.H., and Zoltai, S.C. 1997. Climatic and physiographic controls on wetland type and distribution in Manitoba, Canada. Wetlands **17:** 243-262.

Harris, S.A., French, H.M., Heginbottom, J.A., Johnston, G.H., Ladanyi, B., Sego, D.C., and van Everdingen, R.O. 1988. Glossary of permafrost and related ground-ice terms. National Research Council of Canada Technical Memorandum 142. Ottawa, Canada.

Heginbottom, J.A. 1995. Canada - Permafrost, Plate 2.1, MCR 4177. *In* The National Atlas of Canada. National Resources Canada. Ottawa, Ontario.

Horton, D.G., Vitt, D.H., and Slack, N.G. 1979. Habitats of circumboreal-subarctic sphagna: I. A quantitative analysis and review of species in the Caribou Mountains, northern Alberta. Canadian Journal of Botany **57:** 2283-2317.

Ireland, R.R., Brassard, G.R., Schofield, W.B., and Vitt, D.H. 1987. Checklist of the mosses of Canada. II. Lindbergia **13:** 1-62.

Jeglum, J.K. 1972. Boreal forest wetlands near Candle Lake, central Saskatchewan part II - relationships of vegetational variation to major environmental gradients. The Musk-Ox **11:** 41-58.

Jeglum, J.K. and He, F. 1995. Pattern and vegetation-environment relationships in a boreal forested wetland in northeastern Ontario. Canadian Journal of Botany **73:** 629-637.

Johnson, E.A. 1992. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, Cambridge.

Kenkel, N.C. 1987. Trends and interrelationships in boreal wetland vegetation. Canadian Journal of Botany **65:** 12-22.

Kenkel, N.C. and Orlóci, L. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. Ecology **67:** 919-928.

Kuhry, P. 1994. The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada. Journal of Ecology **82**: 899-910

LaRoi, G.H. and Stringer, M.H. 1976. Ecological studies in the boreal spruce-fir forests of the North American taiga. II. Analysis of the bryophyte flora. Canadian Journal of Botany **54:** 619-643.

Legendre, P. and Legendre, L. 1998. Numerical Ecology. Elsevier Scientific Publishing Company, Amsterdam.

Lewis, F.J. and Dowding, E.S. 1926. The vegetation and retrogressive changes of peat areas ('muskegs') in central Alberta. Journal of Ecology **14:** 317-341.

Lewis, F.J., Dowding, E.S., and Moss, E.H. 1928. T he vegetation of Alberta. II. The swamp, moor, and bog forest vegetation of central Alberta. Journal of Ecology **16:** 19-70.

Lieffers, V.J. and MacDonald, S.E. 1989. Growth and foliar nutrient status of black spruce and tamarack in relation to depth of water table in some Alberta peatlands. Canadian Journal of Forest Research **20:** 805-809.

McCune, B. and Mefford, M.J. 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4. MjM Software Design, Gleneden Beach, Oregon, USA.

Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio **69:** 89-107.

Moss, E.H. 1983. Flora of Alberta. 2nd Edition. *Revised by* J.G. Packer. University of Toronto Press, Toronto.

Moss, E.H. 1953. Marsh and bog vegetation in northwestern Alberta. Canadian Journal of Botany **31:** 448-470.

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. *In* A systems analysis of the global boreal forest. *Edited by* H.H. Shugart, R. Leemans, and G.B. Bonan. Cambridge University Press. pp. 144-169.

Sjörs, H. 1950. On the relation between vegetation and electrolytes in northern Swedish mire waters. Oikos **2**: 241-258.

Slack, N.G, Vitt, D.H., and Horton, D.G. 1980. Vegetation gradients of minerotrophically rich fens in western Alberta. Canadian Journal of Botany **58**: 330-350.

Sollid, J.L. and Sorbel, L. 1998. Palsa bogs as climate indicator-examples from Dovrefjell, South Norway. Ambio **27:** 287-291.

Stotler, R. and Crandall-Stotler, B. 1977. A checklist of the liverworts and hornworts of North America. The Bryologist **80:** 405-429.

Thie, J. 1974. Distribution and thawing of permafrost in the southern part of the discontinuous permafrost zone in Manitoba. Arctic **27**: 189-200.

Turetsky, M.R., Wieder, R.K., Williams, C., Jendro, J., and Vitt, D.H. 2000. Peat chemistry and permafrost in the boreal forest of Alberta: implications for climate change. Écoscience **7:** 379-392.

Vitt, D.H., Achuff, P., and Andrus, R.E. 1975. The vegetation and chemical properties of patterned fens in the Swan Hills, north central Alberta. Canadian Journal of Botany **53:** 2776-2795.

Vitt, D.H. and Chee, W-L. 1990. The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. Vegetatio **89:** 87-106.

Vitt D.H. and Belland, R.J. 1995. The bryophytes of peatlands in continental western Canada. Fragmenta Floristica et Geobotanica **40**: 339-348.

Vitt, D.H., Halsey, L.A., and Zoltai, S.C. 1994. The bog landforms of continental western Canada in relation to climate and permafrost patterns. Arctic and Alpine Research **26:** 1-13.

Vitt, D.H., Halsey, L.A., and Zoltai, S.C. 2000. The changing landscape of Canada's western boreal forest: the current dynamics of permafrost. Canadian Journal of Forest Research **30:** 283-287.

Vitt, D.H., Li, Y., and Belland, R.J. 1995. Patterns of bryophyte diversity in peatlands of continental western Canada. The Bryologist **98:** 218-227.

Vitt, D.H. and Slack, N.G. 1984. Niche diversification of *Sphagnum* relative to environmental factors in northern Minnesota peatlands. Canadian Journal of Botany **62:** 1409-1430.

Washburn, A.L. 1980. Permafrost features as evidence of climatic change. Earth-Science Reviews **15:** 327-402.

Wein, R.W. 1983. Fire behaviour and ecological effects in organic terrain. *In* The Role of Fire in Northern Circumpolar Ecosystems. *Edited by* R.W. Wein, and D.A. McLean. John Wiley and Sons, New York.

Whittaker, R.H. 1972. Evolution and the measurement of species diversity. Taxon **21:** 213-251.

Williams, P.J. and Smith, M.W. 1989. The Frozen Earth. Cambridge University Press, New York.

Woo, M.-K., Lewkowitcz, A.G., and Rouse, W.R. 1992. Response of the Canadian permafrost environment to climatic change. Physical Geography **13:** 287-316.

Zar, J.H. 1999. Biostatistical Analysis, 4th Edition. Prentice Hall, New Jersey.

Zoltai, S.C. 1993. Cyclic development of permafrost in the peatlands of northwestern Alberta, Canada. Arctic and Alpine Research **25:** 240-246.

Zoltai, S.C. 1972. Palsas and peat plateaus in central Manitoba and Saskatchewan. Canadian Journal of Forest Research **2:** 291-302.

Zoltai, S.C. and Tarnocai, C. 1971. Properties of a wooded palsa in northern Manitoba. Arctic and Alpine Research **3:** 115-129.

CHAPTER 4:
BOG DEVELOPMENT AFTER LOCALIZED PERMAFROST DEGRADATION IN BOREAL WESTERN CANADA

4.1 INTRODUCTION

Peatland development has proceeded in western Canada through the Holocene under the influence of a changing climate. In continental western Canada (Alberta, Saskatchewan, and Manitoba) peatlands began forming about 9000 years BP, and reached their present southern limit by 2000 years BP (Halsey *et al.* 1998). Peatland development reconstructed via pollen and macrofossil histories and radiocarbon dating has been well studied in this region (Vitt and Kuhry 1992). Allogenic factors, especially climate, local physiography, and soils (Halsey *et al.* 1997) and such autogenic factors as peat accumulation and acidification by *Sphagnum* (Kuhry *et al.* 1993; Nicholson and Vitt 1990) have been shown to affect peatland development. Currently, peatlands form a major part of the western Canadian boreal and subarctic landscape, covering 21% of continental western Canada (Vitt *et al.* 1998).

Within the Discontinuous Permafrost Zone, permafrost is most common in peatlands (Brown 1968). Permafrost distributions have been dynamic through the Holocene, and Zoltai (1995) suggested that much of the Discontinuous Zone was displaced north of its present position at 6000 years BP, and that southern expansion of permafrost in peatlands followed boreal and subarctic peatland expansion. Presently, permafrost landforms in peatlands vary in size, and can be classified as either peat plateaus (spatially extensive peatlands completely underlain by frozen ground) or as isolated frost mounds in mostly unfrozen peatland (Brown 1968) that I call localized permafrost peatland. Localized permafrost occurs in the south of the Discontinuous Zone, and is the southernmost permafrost landform type in peatlands (Chapter 2). Permafrost in peatlands is melting across continental western Canada, creating collapse scars

in peat plateaus and internal lawns in localized permafrost peatlands (Vitt *et al.* 1994).

The influence of permafrost on peatland development has been described in a few papers, although little is known about its effect on localized permafrost peatlands. Most paleoecological studies have concentrated on Holocene permafrost aggradation (Lavoie and Payette 1995; Kuhry 1998) and dynamics in peat plateaus and collapse scars (Zoltai 1993; Camill 1999). Using plant macrofossil evidence in near-surface collapse scar peat, Zoltai (1993) showed that several cycles of permafrost melt and redevelopment have occurred over the last 2,000 years in northwestern Alberta. Peat accumulation and community change proceed quickly in collapse scars, from wet communities to dry communities able to support trees in less than 100 years (Camill 1999). Plant community changes in internal lawns resulting from localized permafrost collapse have not been investigated in detail in western Canada, with only two internal lawns briefly described by Vitt *et al.* (1994).

Bog development following localized permafrost degradation is strongly influenced by peat accumulation in an oligotrophic environment. Modern vegetation and environmental conditions of internal lawns in bogs range from dry *Sphagnum fuscum* hummocky surfaces with stunted black spruce, to very wet treeless *S. riparium* carpets. Modern variability in internal lawn vegetation can be attributable to either asynchrony of degradation events (wetter sites are younger) or to differences in the magnitude of collapse disturbance. My objective in this chapter is to investigate the latter explanation, and describe plant community histories following localized permafrost collapse in ombrogenous peatlands. Specifically, I address the question: are all internal lawn developmental histories the same (i.e. does localized permafrost always result in collapse to below the water table, followed by unidirectional succession of species to *Sphagnum fuscum* hummocky communities)?

4.1.1 Study Sites

To capture variability at the regional level, three peatlands were selected for study within the distribution of localized permafrost bogs in western Canada. Localized permafrost bogs were named after their nearest map locality and included Anzac bog, AB, Patuanak bog, SK and Moose Lake bog, MB (Figure 4-1). Sites were selected from aerial photographs of the region to have distinct localized permafrost landforms (treed frost mounds and internal lawns), reasonable accessibility, and to span the geographic range of localized permafrost bogs. Sites are located near the southern limit of permafrost. Both localized frost mounds and internal lawns occur in the study peatlands (Table 4-1).

4.2 METHODS

4.2.1 Field sampling

To fully explore the variability in peatland development within internal lawns, between internal lawns from the same peatland and between internal lawns from different peatlands, three internal lawns from each peatland were randomly chosen from the total accessible population of internal lawns. A single peat core was extracted from two locations in each lawn, selected to capture the range of the internal lawn's developmental history. Coring locations were chosen based on the height of the surface relative to the water table and the composition of the surface vegetation, with one core taken from the wettest area and the other from the driest area of the internal lawn. Care was taken to avoid the edges of the feature where permafrost conditions were marginal. Cores were extracted using a stainless steel 7cm x 7cm x 1m box sampler (Fig. 4-2) modified from Jeglum et al. (1994). Cores were subsectioned in the field into 10 cm lengths, packaged into 1 m sections of plastic eavestroughing, and wrapped in plastic film for transport. Sylvic peat consisting of dark, well humified organic material including spruce macrofossils (needles, wood, bark, twigs) was present in each core extracted. This sylvic peat represents vegetation and environmental

conditions from the pre-existing frost mound surface, and its presence ensured that the complete post-degradation history was captured in each core. In the laboratory, cores were kept frozen until processed.

4.2.2 Peat core analyses

Beginning with the sylvic layer, peat cores were sampled every 10 cm or at major changes in the peat stratigraphy, through to the near surface peat. Samples were extracted semi-frozen with a #12 brass cork borer (inner diameter = 1.77 cm), and cut into 3 cm^3 and 5 cm^3 subsamples for macrofossil and physical analyses, respectively.

Macrofossil subsamples were screened using two sieve sizes; 500 μm to separate large material and intact bryophyte branches from smaller material and leaves, and 150 μm to separate small material from fine debris. Macrofossil remains from the 500 μm screening were dispersed in distilled water on a petri plate and identified using dissecting and compound microscopes. Assemblages were verified by identifying a small grab of material (loose bryophyte leaves) from the 150 μm screening. Species names follow Moss (1983) for vascular plants, Ireland *et al.* (1987) for mosses, and Stotler and Crandall-Stotler (1977) for hepatics. Macrofossil abundance in each assemblage was estimated as relative percent cover on the petri plate. Material captured on both screen densities following sieving was air dried and weighed, and used to determine the degree of decomposition (in this case the 'intactness' of plant remains) of the peat subsample. This was calculated as the ratio of the weight of material from the 150 μm and 500 μm screens, and results in an index (that I call '150:500 sieve ratio' with possible values ranging from zero to infinity) where larger values indicate more decomposition or separation of leaves from branches and stems.

Subsamples for physical analyses were dried for 24 hours at 65°C and weighed to determine bulk density. Oven-dried samples were then ashed at 550°C for 4 hours and re-weighed to determine the loss of organic matter on ignition, expressed as gravimetric percent ash.

4.2.3 Data analysis

Assemblages were grouped and classified by agglomerative cluster analysis using the Bray-Curtis dissimilarity measure linked by the UPGMA method (Legendre and Legendre 1998). Assemblages from all cores were compared and interpreted using multivariate ordination (Gordon and Birks 1974; Prentice 1980). Pathways of community change following permafrost melt were illustrated by first ordinating all assemblages by correspondence analysis (Hill 1974). Successional vectors connecting assemblages in order for each core were then superimposed onto the ordination space. Multivariate analyses were implemented in PC-ORD (McCune and Mefford 1999).

The bryophyte component of each post-collapse macrofossil assemblage was used to reconstruct the paleoenvironmental history of peatland surface relative to water table for each core. Weighted averaging (ter Braak 1995) was used to calculate species scores from a modern data set and an inferred height above water table value for each assemblage. This technique has performed well for lake pH reconstruction from fossil diatoms (Birks *et al.* 1990) and has also been applied to reconstruction of peatland pH and wetness histories from fossil bryophytes (Janssens *et al.* 1992; Kuhry *et al.* 1993). Species scores for bryophytes in macrofossil assemblages were determined from quadrat and relevé data with associated height above water table values from peatland sites across continental western Canada, east of the Rocky Mountains from Gignac *et al.* (1991). Species scores are provided in Table 4-2. Inferred surface wetness values are accurate within the range of measurement in the original wetland data set. Since localized treed frost mounds are elevated landforms that can have

surfaces over 2 m above water table (Zoltai and Tarnocai 1971; Zoltai 1972), values were not computed for sylvic assemblages.

4.3 RESULTS

4.3.1 Plant macrofossils

In total, 137 macrofossil assemblages were determined in the 18 cores from the three study bogs (Appendix 3). Each assemblage was dominated by one or two main components. A sylvic peat layer occurred between 34 and 85 cm depth in each core. The macrofossil components of the sylvic layer were consistent with vascular and nonvascular vegetation of existing treed frost mounds in each of the study peatlands (Chapter 3), including abundant *Picea* needle, bark and twig litter, lichen remains, *Pleurozium schreberi*, *Dicranum* spp. and unidentifiable organic debris. *Sphagnum* was lacking in most sylvic assemblages, but when present always consisted of well humified *S. fuscum* in association with abundant *Picea* macrofossils. Evidence of fire (charred macrofossil remains) was encountered at the transition from sylvic to *Sphagnum* peat in seven of the 18 cores, and was present in at least two of the six cores from each peatland. Charcoal was never found in both cores from the same feature, and in six of its seven occurrences was in the wet location core. Post-collapse assemblages lacked sylvic components, were always dominated by *Sphagnum*, and were very well preserved (lacked unidentifiable debris). *Drepanocladus fluitans* was sometimes abundant in early post-collapse assemblages (up to 20% of macrofossil abundance) particularly at the Patuanak site, and was missing from Moose Lake assemblages. Roots from ericaceous shrubs and graminoids were common and sometimes dominated assemblages. Root components are not a representative part of communities present when peat was deposited (roots growing down from the surface into older peat). Since my objective was to reconstruct changes in communities and environmental conditions when peat was formed, ericaceous and graminoid roots were excluded from multivariate analyses of macrofossil data.

Post-degradation *Sphagnum*-dominated assemblage succession was variable, both within and between internal lawns. *Sphagnum* species can persist through the entire macrofossil record (*S. magellanicum*, Fig. 4-3A), or succeed each other over short distances (Fig. 3B) in cores taken from the same internal lawn. Cluster analysis of macrofossil abundances obtained from all core subsamples provided division of assemblages (the seven most distinct clusters) that were named for their dominant components (Fig. 4-4). These macrofossil assemblage groups are summarized for all cores by their depth in Figure 4-5. Ordination by CA separated *Sphagnum*-dominated assemblages well along the first axis (eigenvalue = 0.82; Fig. 4-6). Axis 2 generally separated sylvic from *Sphagnum*-dominated assemblages (eigenvalue = 0.73).

Successional vectors superimposed on the CA ordination diagrams illustrate that peatland development does not always follow the same sequence following frost mound collapse. Although pathways generally follow a similar trajectory eventually leading to drier communities (after peat accumulation and compaction), initial communities following colonization and establishment after melt can differ (Fig. 4-7). General patterns are evident in these diagrams. Sylvic peat assemblages deposited on the pre-existing treed frost mounds were most distinct (as shown by their position on the diagram) in the Anzac and Patuanak cores. Moose Lake sylvic assemblages were less distinct and sometimes clustered with *S. fuscum* assemblages due to their greater *Sphagnum* component, although strongly sylvic assemblages were also present at this site (Moose Lake internal lawn 3). There is a great deal of variability within internal lawns. Bog development can follow similar sequences in both wet and dry locations, as shown in the cores from Anzac internal lawn 3. However, different areas of the same internal lawn can have differing initial communities following collapse (Anzac internal lawn 1). Internal lawns from both Anzac and Patuanak included collapse to *S. riparium* communities, while the Moose Lake internal lawn cores did not include *S. riparium* dominated communities (although it was present). Succession from *S. riparium* to *S. fuscum* communities occurred more

frequently at Anzac, whereas *S. riparium* communities remained dominant throughout the wet location core histories from Patuanak.

4.3.2 Quantitative reconstruction of water table

Height above water table reconstruction indicates that different localized permafrost landforms collapse to different levels relative to water table (Fig. 4-8). Variability within individual internal lawns was also evident, as cores from the same internal lawn had different wetness histories. Permafrost collapse can create very wet conditions in localized permafrost bogs, and the lowest reconstructed values were about 1 cm above water table.

4.3.3 Physical peat characteristics

The three assemblages that were dominated by Cyperaceae leaves are subsamples that likely captured the base of *Eriophorum vaginatum* tussocks from permafrost mounds (when they included sylvic components) or internal lawns (when they included *Sphagnum* components), and have been excluded from this section. Percent ash and bulk density of peat were high in the sylvic permafrost layers (Fig. 4-3; Fig. 4-9), compared to lower values for *Sphagnum*-dominated peat layers. The weight ratio of plant remains captured by the 150 and 500 μm sieves was high for sylvic peat and indicates a high degree of humification. The *Sphagnum* groups show increased intactness with increased mean height above water table values for dominant components (*S. riparium* - *S. fuscum* series) that is associated with depth and age in internal lawn cores (*S. riparium* often the older plants in the peat, deposited during wetter newly collapsed periods).

4.4 DISCUSSION

Western Canadian bogs that have not been affected by permafrost have comparatively simple bryofloras, with about half as many species as fens (Vitt *et al.* 1995a). Regionally across western Canada, *Sphagnum* species distributions across all peatland types are limited mostly by water chemistry and climatic gradients (Gignac and Vitt 1990). However, continental bogs are much less variable than geogenous peatlands in their water chemistry (Vitt *et al.* 1995b), and Belland and Vitt (1995) found that the main limiting gradients in continental western Canadian ombrogenous peatlands were dryness, shade and pH. Internal lawns throughout our study sites show little variability in pH (mean ± s.d. = 4.03 ± 0.13, n = 45) relative to the range of conditions seen across peatland types in western Canada (bog = 3.96 ± 0.07; extreme-rich fen = 6.88 ± 0.30 (Vitt *et al.* 1995b)). Shade has little influence on internal lawn community succession as newly collapsed features drown *Picea mariana* populations that cannot re-establish until drier conditions emerge following peat accumulation and compaction. Even once conditions are dry enough to allow *Picea* to germinate and establish, initial tree growth is likely suppressed on modern internal lawn surfaces that are closer to the water table than bog surfaces (cf. Lieffers and Rothwell 1986). The nine internal lawns cored in this study had very low *P. mariana* cover (mean = 1.2 ± 1.8%). Thus, internal lawn community succession is most affected by surface dryness that changes with peat accumulation and internal lawn age.

4.4.1 Plant macrofossils

The macrofossil groups identified by the cluster analysis in conjunction with the CA ordination provide a readily interpretable diagram of plant community change following permafrost melt (Fig. 4-6). The relative location of assemblage points along the first CA axis follows the height above water table gradient in *Sphagnum*-dominated internal lawns. Decreases in assemblage axis scores (from positive to negative) represent species changes due to increases in surface

dryness that occur as peat accumulates. The position of assemblages along this axis also agrees with independent species scores from Table 4-2. Axis 2 can be interpreted as a complex gradient that relates to both greater dryness and shade towards the top of the diagram, and represents increasing influence of permafrost conditions (with greater *Picea*, lichen, and feathermoss, and *Dicranum* spp. components and exclusion of *Sphagnum*).

Macrofossils present in assemblages immediately above sylvic peat layers show that newly collapsed frost mounds can have different initial communities determined by variability in post-collapse environmental conditions. This variability is evident within lawns (Fig. 4-3; Fig. 4-7), and indicates that different parts of the same internal lawn can have different initial community types. The longevity of assemblage types in the record also varies; in some cores assemblage types succeeded each other quickly (Fig. 4-7 - Anzac internal lawn 1, dry location core), and other cores showed prolonged periods of similar macrofossil composition (Patuanak internal lawn 1 and 2, wet location cores). The wet, treeless conditions that characterize internal lawns in boreal peatlands can thus be of different extent and longevity, depending on the local conditions created by permafrost melt. This variability is also evident in collapse scars in peat plateaus, as Zoltai (1993) reported different *Sphagnum* assemblages in different collapse scar periods from peat plateaus that show several permafrost formation/melt cycles.

4.4.2 Quantitative reconstruction of water table

Reconstructed height above water table values indicate that localized permafrost melting collapses surfaces to variable positions relative to the local water table. These reconstructed wetness histories complement the results of the CA diagram vectors, and support the major trends identified in the ordination analysis. Although reconstructed wetness values were as low as 1 cm, ground observations from the peatland sites indicate that recently collapsed surfaces can be sunken below the water table, sometimes by more than 20 cm. The

discrepancy between the reconstructions and ground observations is due to the actual internal lawn conditions following melt being out of the range of conditions from the calibration data set (minimum value = 0 cm). Reconstructed values therefore represent maxima for height above water table, that accurately would often be negative. Overall, reconstructed height above water table changes are best interpreted as an index showing relative changes in internal lawn history, rather than as accurate values.

Wet-adapted *Sphagnum riparium/Drepanocladus fluitans* communities can persist throughout post-collapse cores (Patuanak cores 1 and 2, wet sites) and shows that frost mound collapse can be substantial, and that carpet communities and conditions can last for some time. In these situations, rapid *Sphagnum* succession is likely postponed until surfaces emerge to heights closer to individual species optima (Table 4-2). Height above water table reconstructions of entire peatland histories in other studies show that the change from brown moss dominance to *Sphagnum* is associated with large increases in surface height above water table (Kuhry *et al.* 1993; Janssens *et al.* 1992; Nicholson and Vitt 1990). The low, near water table values calculated from *Sphagnum* assemblages here are closer to geogenous rich fen (brown moss) values in these studies (and are often lower), though internal lawns retain the low pH values consistent with bogs and acidic poor fens (Vitt *et al.* 1995b). This suggests that localized permafrost collapse in bogs create the wettest conditions experienced in continental ombrogenous peatlands, and these physically resemble carpet/pool habitats of oceanic bogs (Damman 1977; Gignac and Vitt 1990; Vitt et al. 1990).

4.4.3 Fire and localized permafrost melt

Fire is the principal cause of natural disturbance in the Canadian boreal forest (Wein and MacLean 1983; Johnson 1992; Payette 1992), and has an influence on peatland vegetation and development (Wein 1983; Kuhry 1993; Zoltai *et al.* 1998). All three of my study sites show evidence of past fire in the

form of charcoal macrofossils that, when present, were always located at the boundary between sylvic frost mound peat and the overlying *Sphagnum* internal lawn peat (Fig. 4-5). This suggests that permafrost degradation occurs when fire burns the vegetation and surface peat of frost mounds in localized permafrost bogs. Peat plateaus have been shown to resist degradation following fire (Thie 1974) or to redevelop permafrost in peat plateau – collapse scar cycles initiated by fire (Zoltai 1993). Localized permafrost is more susceptible to degradation after disturbance due to its southern distribution and the warmer climates in which it occurs, and no evidence exists for its resistance to fire or its redevelopment. Localized permafrost below surfaces that are burned likely always degrades, and probably does not reform, in the south of its distribution.

Charcoal layers were never found in both cores from the same internal lawn. Although this may be a shortcoming of the peat core sampling design, as non-contiguous sample locations may have missed thinner charcoal layers, it may also be explained by two historical scenarios. First, localized fire may have initiated degradation that triggered subsequent melt of surrounding unburned areas, resulting in collapse of the whole feature within a relatively short time. A patchy fire pattern may be related to the fuel characteristics of the frost mound vegetation. Areas with thicker frost lenses have taller, denser *Picea* cover (Zoltai and Tarnocai 1971) that may be more susceptible to fire than less dense areas of the same frost mound. Once melt begins in the burned area it may continue due to instability along the melting front that thins permafrost lenses and increases wetness and thermal conductivities, that may spread thaw into unburned areas. Although permafrost degradation can be halted by specific surface vegetation and soil conditions in peat plateaus (Camill and Clarke 1998), localized permafrost melt is likely difficult to stop in warmer climates. This scenario is supported by the occurrence of six of seven charcoal layers in the wet location cores. The larger amount of vertical collapse relative to the water table (the wet location in the internal lawn) is caused by a lower vertical peat accumulation rate on the frost mound relative to that of the surrounding bog, and is influenced by

the same environmental conditions that increased tree growth. Loss of additional peat depth due to the burning of surface peat also adds to the degree of collapse. The second scenario involves two distinct permafrost degradation events. An early period of slower melt may have occurred, resulting from thermal disequilibrium with climate (though possibly initiated by a localized disturbance such as tree throw). This was followed by a second period of rapid degradation when fire burned the remaining frost mound and skipped the wet internal lawn that was formed previously. All wet site cores had a consistently shallower or equivalent depth sylvic peat layer compared to the dry site core in each of the nine internal lawns studied. This suggests that wet coring sites may indeed represent younger collapse than dry coring sites and supports the second scenario. However, depth may not be a good direct surrogate for age in collapse scars and internal lawns, as rates of peat accumulation are variable over the age of these peat deposits (Camill 1999; Turetsky et al. 2000). Resolution of these two scenarios could be accomplished by careful dating of collapse events by ^{210}Pb or dendrochronological techniques.

4.4.4 Physical peat characteristics

Peat deposited on the pre-existing frost mound surface has very different physical qualities than the *Sphagnum* post collapse peat. High bulk density values in sylvic peat indicate a higher degree of decomposition in these dry non-wetland environments. Likewise, the high ash content in these layers represents the combined effects of increased humification as well as possible intrinsic differences in the mineral content of the species (Tolonen 1984). Turetsky *et al.* (2000) reported similar bulk density and ash values for localized frost mounds in Alberta, and Camill (1999) showed similar values for peat plateaus in Manitoba. The post-collapse *Sphagnum*-dominated assemblages had much lower values for percent ash and bulk density than the sylvic assemblages, consistent with near-surface *Sphagnum* deposits from across the region (Kuhry 1997; Kuhry *et al.* 1992), other internal lawns (Turetsky *et al.* 2000), and collapse scars (Camill 1999).

Sphagnum assemblage groups have decreasing 150:500 sieve ratios that correspond to the wetness gradient, where wet-adapted groups have larger sieve ratios than the drier-adapted groups. This is largely due to time since collapse relationships, as dry-adapted plants like *S. fuscum* occur later in the development history and are therefore more intact than wet-adapted species that usually occur immediately following collapse (have spent more time as peat). However, a species-specific effect is also present, as leaves from species of *Sphagnum* section Cuspidata (*S. angustifolium*, *S. riparium*, and *S. jensenii*), appear to become separated from stems and branches more readily than more resilient species from sections Acutifolia (*S. fuscum and S. russowii*) or Sphagnum (*S. magellanicum*). The slightly higher value in the *S. russowii* dominated assemblages is likely due to the inclusion of more section Cuspidata species than the *S. magellanicum* and *S. fuscum* assemblages.

4.4.4 Conclusions

Localized permafrost has been degrading over the last 150 years in boreal continental western Canada creating internal lawns in peatlands (Vitt *et al.* 1994). It has been argued that the current distribution of localized permafrost is in disequilibrium with modern climate (Halsey *et al.* 1995) and melt is continuing across the region. Global temperatures are predicted to increase in the western Canadian boreal forest (Boer *et al.* 2000). Recent estimates suggest that less than half of the currently vulnerable permafrost has collapsed across the region, and the area of climatically sensitive permafrost will increase with warmer temperatures (Vitt *et al.* 2000). Future ecological changes resulting from permafrost melt across the region will thus be affected by 1) increased rates of permafrost melt (Thie 1974; Engelfield 1995; Camill and Clark 1998), 2) increased area of vulnerable permafrost (Vitt *et al.* 2000, Anisimov and Nelson 1997), and 3) the magnitude of disturbance caused by landform collapse as shown in this paper. Specifically, the macrofossil histories of the 18 peat cores studied in this chapter have lead to the following conclusions:

1) In the internal lawns studied here, peatland development and *Sphagnum* community succession proceeded along a similar trajectory from wet to dry following localized permafrost melt, although initial communities and the longevity of communities are variable.

2) Plant community succession is markedly variable at the local scale within individual internal lawns, as well as variable regionally within and between peatlands.

3) Localized permafrost landforms collapsed to variable positions relative to peatland water tables producing different degrees of disturbance following permafrost melt. Dry internal lawn surfaces on the present landscape may have started very wet or relatively dry.

4) Fire resulted in degradation of the permafrost that occurred below burned surfaces in the localized permafrost bogs studied, while other surfaces collapsed without a fire event.

Table 4-1. Characteristics of the three localized permafrost bogs sampled. See Table 3-1 for additional details.

		Anzac Bog, AB	Patuanak Bog, SK	Moose Lake Bog, MB
	Location	56.47° N, 111.04° W	55.84° N, 107.68° W	55.08° N, 99.95° W
Climate	Mean annual temperature (°C)	-0.4	-1.0	-1.2
	Mean annual precipitation (mm)	471.9	443.9	495.6
Peatland	Total bog area (km^2)	6.97	1.33	4.07
	Extent of degradation (% by area)	60.3	65.5	53.2

Table 4-2. Weighted mean height above water table (HAWT) scores for abundant bryophytes found in macrofossil assemblages. Bryophyte species scores were calculated from modern peatland vegetation sampled across continental western Canada (see Gignac *et al.* 1991).

Species	Weighted mean HAWT (cm)	Standard deviation (cm)	n
Dicranum spp.	38	17.7	254
Drepanocladus fluitans	1	1.8	31
Mylia anomala	32	12.3	120
Pleurozium schreberi	38	14.6	208
Pohlia nutans	22	9.6	34
Polytrichum strictum	31	13.7	185
Sphagnum angustifolium	21	8.9	207
Sphagnum fuscum	36	12.6	239
Sphagnum jensenii	1	0.7	11
Sphagnum magellanicum	25	7.8	151
Sphagnum riparium	1	6.2	22
Sphagnum russowii	23	10.2	13

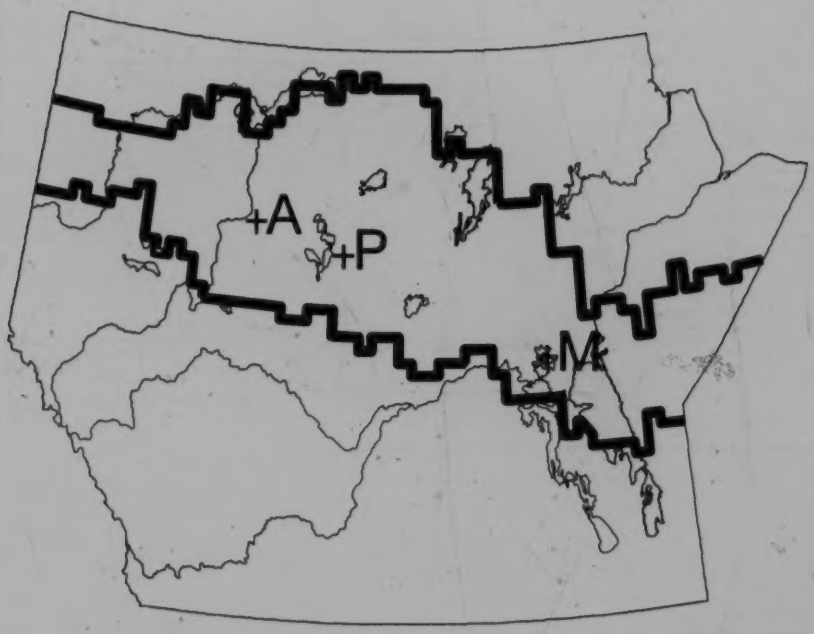


Fig. 4-1. Continental western Canada (Alberta, Saskatchewan, and Manitoba) with the outline of the localized permafrost peatland region (Chapter 2) and location of study sites; Anzac, AB (A), Patuanak, SK (P), and Moose Lake, MB (M).

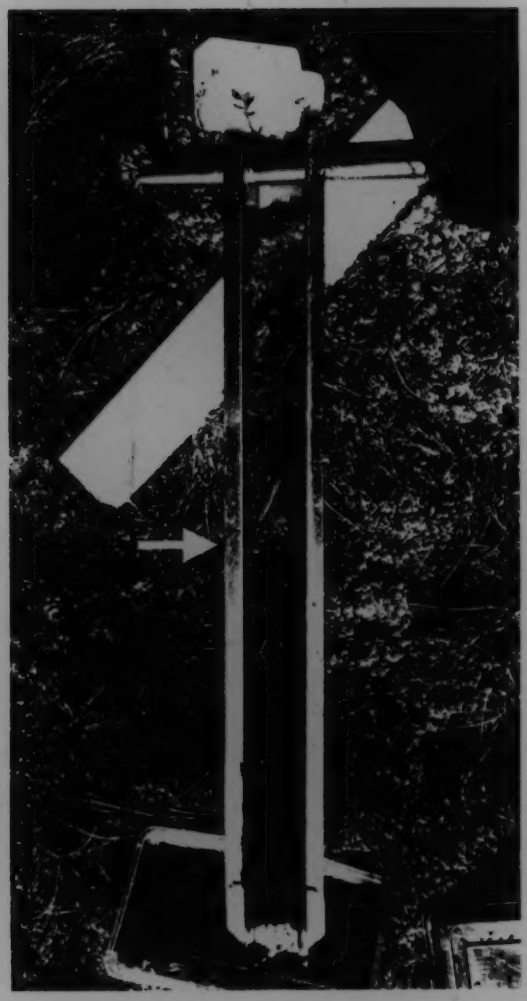


Fig. 4-2. Box sampler core from Patuanak, SK. Light, well preserved *Sphagnum* peat and dark, well humified sylvic peat are separated by a sharp collapse boundary (white arrow).

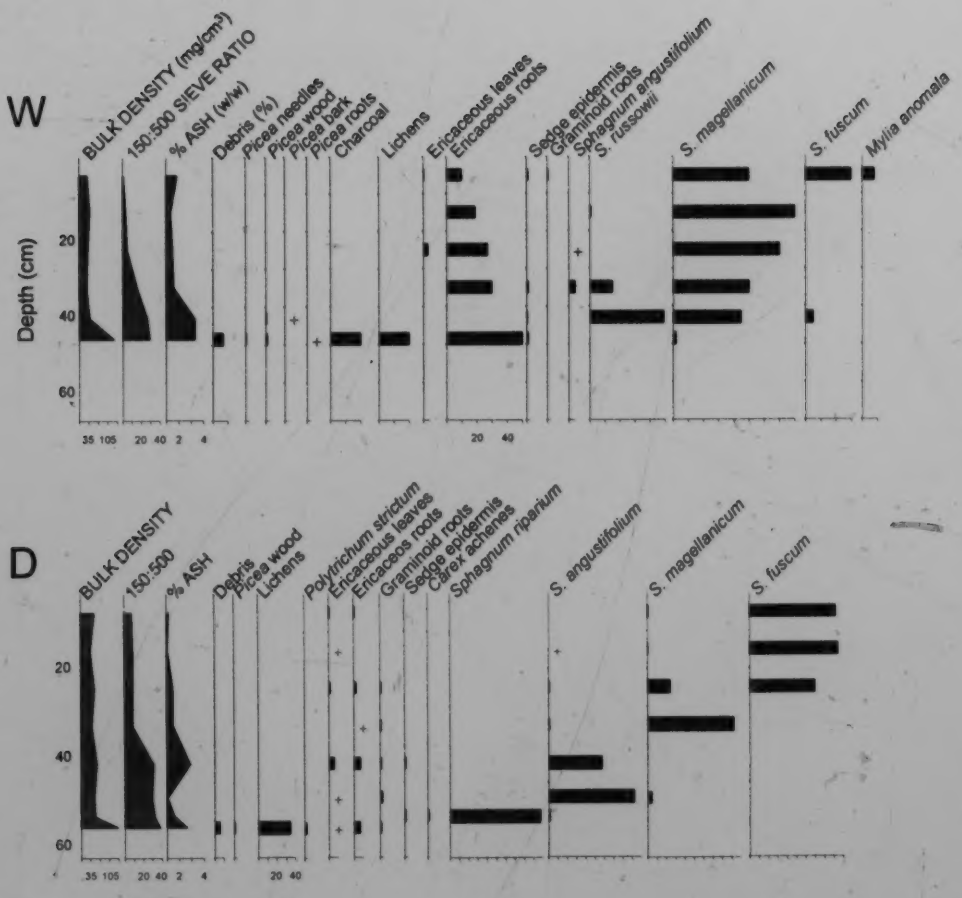


Fig. 4-3. Detailed macrofossil stratigraphy from two cores (W = wet site; D = dry site) from internal lawn 1, Anzac, AB bog. Cores show different successional histories within the same internal lawn. Bars indicate macrofossil abundance (percent frequency). Plus signs (+) show macrofossil presence at less than one percent abundance.

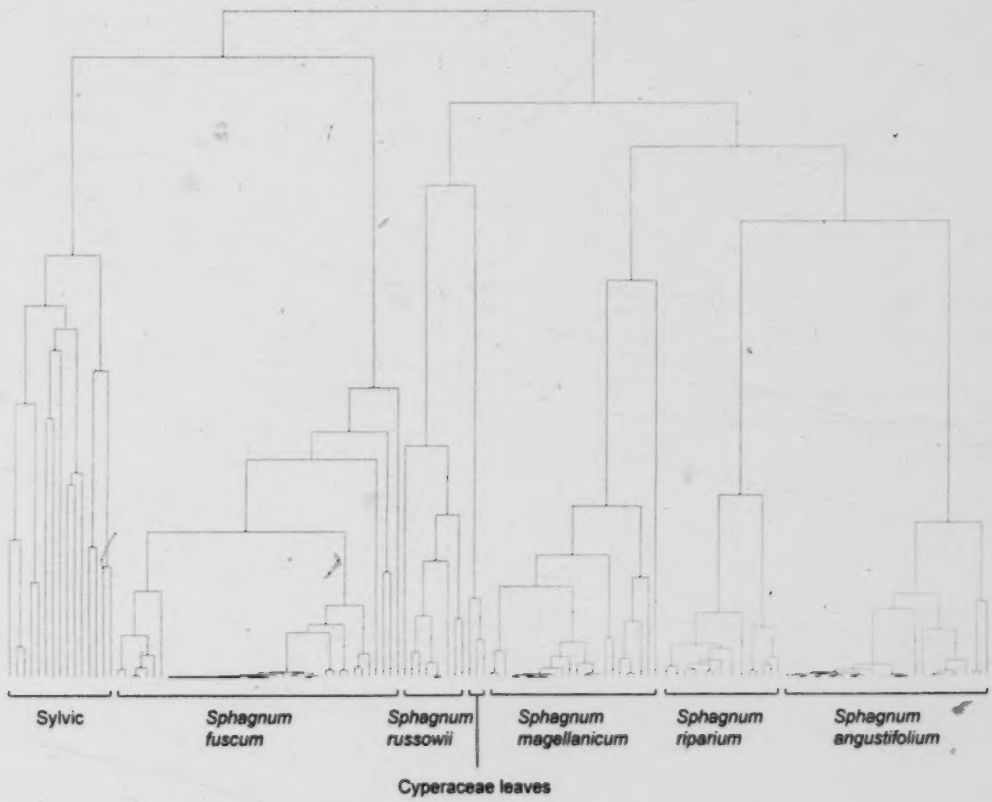


Fig. 4-4. Bray-Curtis UPGMA cluster analysis and classification of 137 macrofossil assemblages. Assemblage groups are named for the dominant species present. Ericaceous and sedge root macrofossil abundances were excluded from the data before analysis.

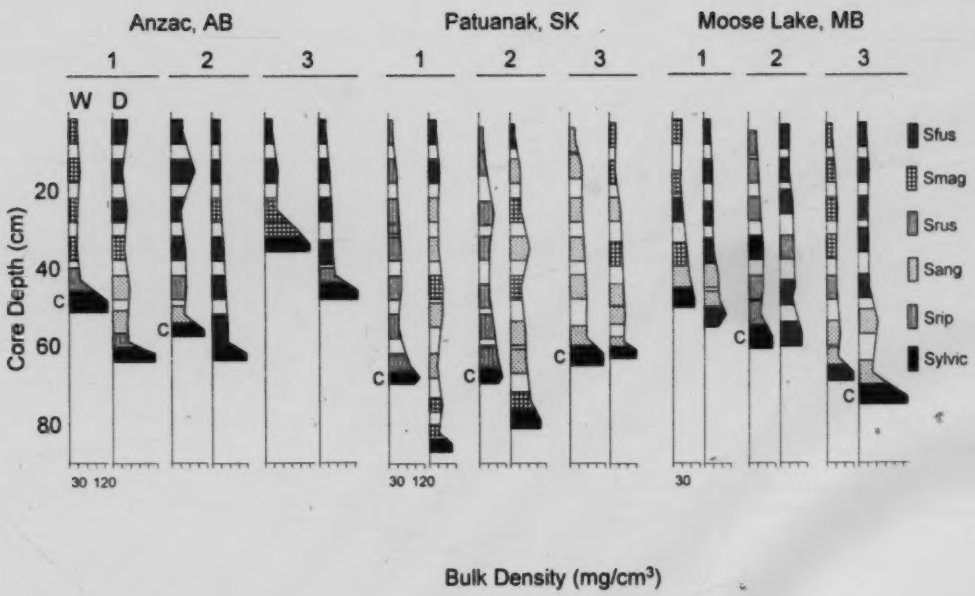


Fig. 4-5. Macrofossil assemblage groups and peat bulk density profiles for internal lawn cores. Two cores were extracted from each of three internal lawns in each of three peatlands (total 18 cores). Numbers above cores correspond to individual internal lawns. Wet site cores (W) are to the left and dry site cores (D) are to the right below each internal lawn number. The vertical dimension of peat core samples (centred on its extracted depth) is greatly exaggerated for clearer viewing. Bulk density values on the horizontal axis are in 30 mg/cm^3 increments. The symbol 'C' shows the presence of charcoal in macrofossil assemblages.

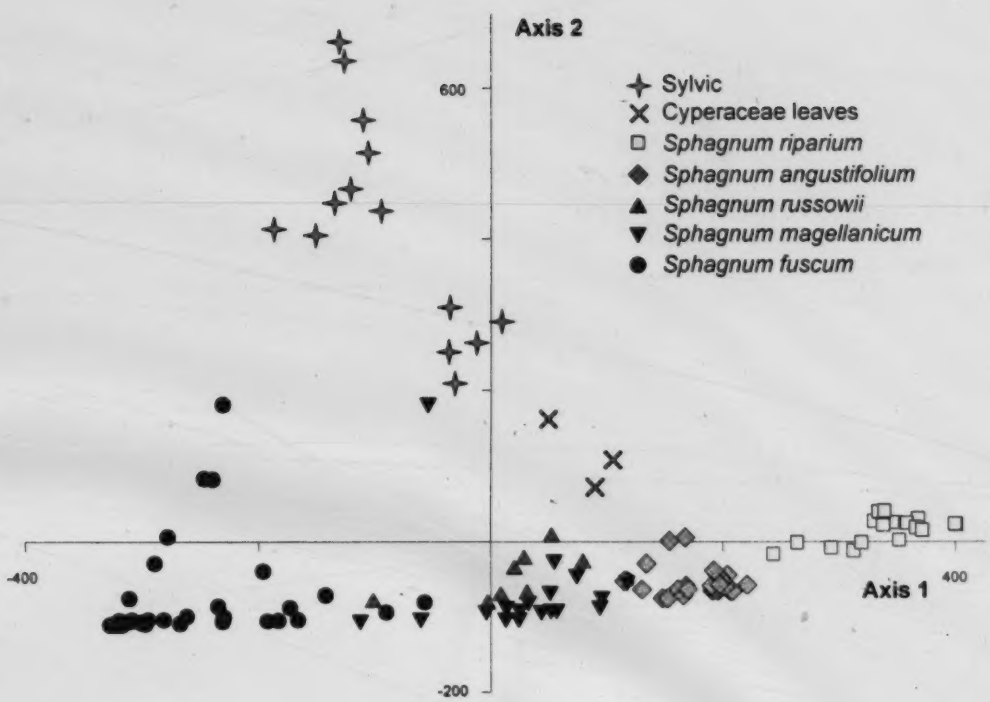


Fig. 4-6. Correspondence analysis ordination of macrofossil assemblages from 18 cores. Symbols and legend correspond to macrofossil groups from the cluster analysis.

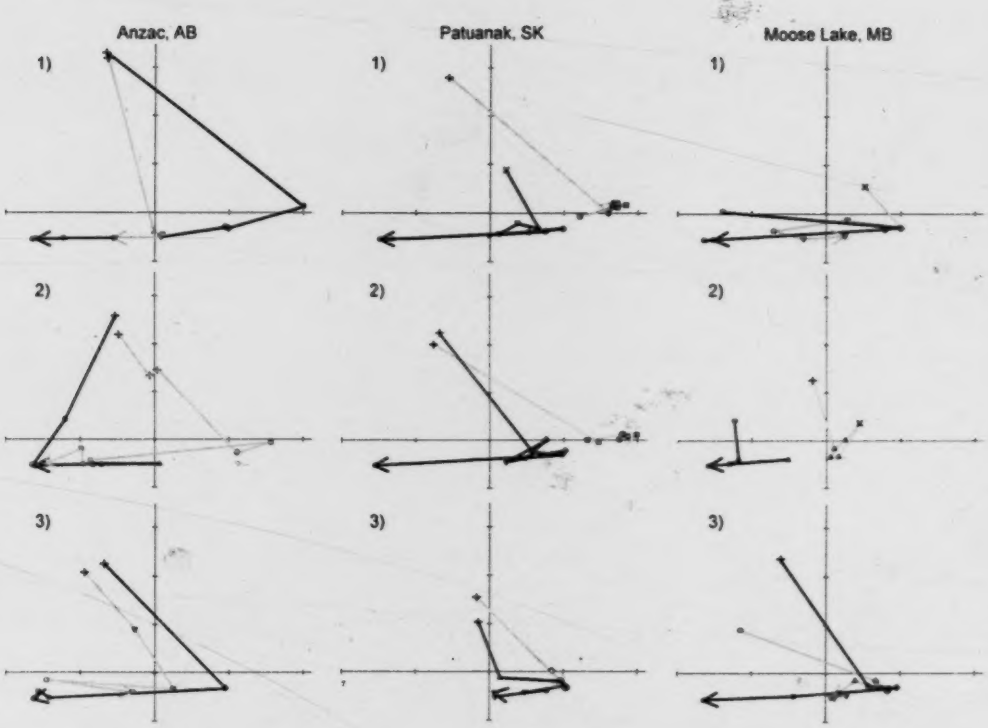


Fig. 4-7. Pathways of community change following permafrost degradation drawn as successional vectors on the ordination diagram from Figure 4-6. Each diagram shows the pathway from both cores from each internal lawn; black lines represent cores taken from present wet locations of internal lawn surfaces, light lines are cores taken from present dry locations. Symbols show cluster analysis groups and follow Fig. 4-6.

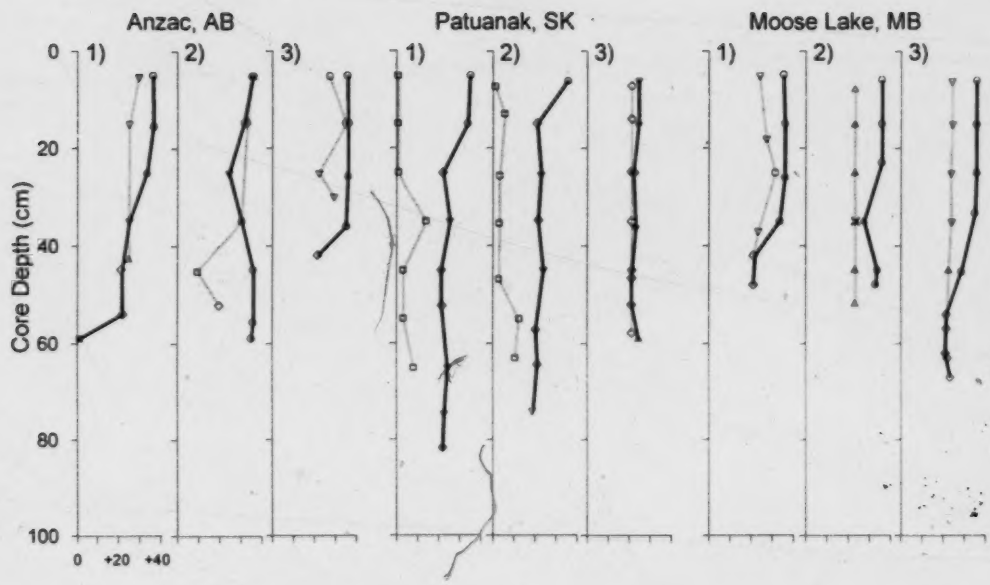


Fig. 4-8. Reconstructed past changes in surface height above water table following permafrost collapse in 18 cores from three study sites across western Canada. Only the post-collapse reconstructed values from macrofossil assemblages (i.e. those above sylvic layers) are shown. Black lines represent cores taken from present wet locations of internal lawns surfaces, light lines are cores taken from present dry locations. Height above water table values along the horizontal axis of each plot is shown in centimeters.

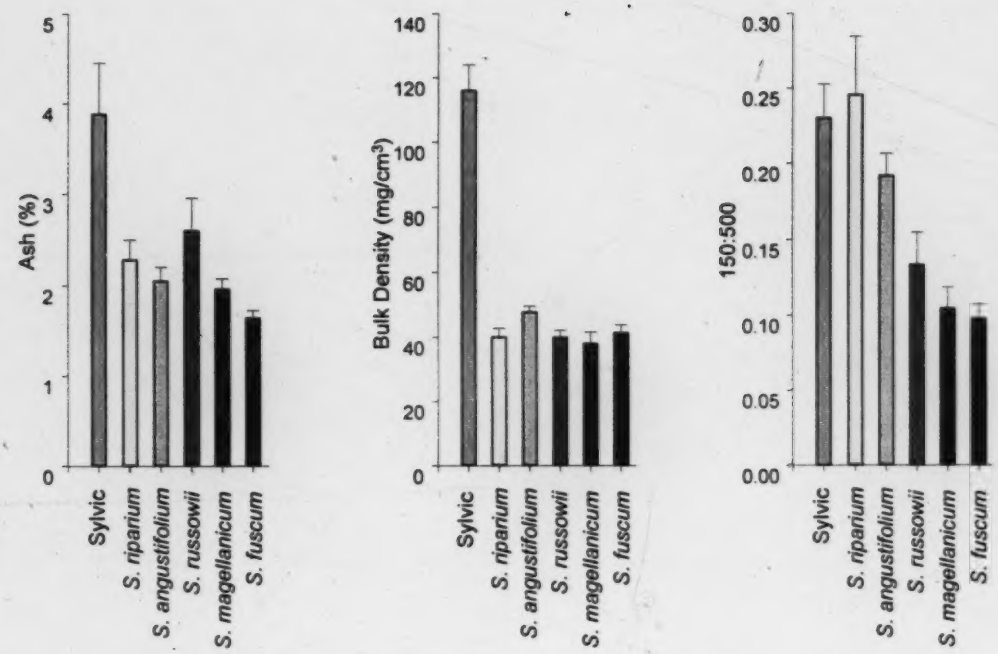


Fig. 4-9. Mean values of peat physical characteristics by macrofossil cluster group. Error bars show standard error of the mean.

4.6 LITERATURE CITED

Anisimov, O.A. and Nelson, F.E. 1997. Permafrost zonation and climate change in the Northern Hemisphere: results from transient general circulation models. Climatic Change **35:** 241-258.

Belland, R.J. and Vitt, D.H. 1995. Bryophyte vegetation patterns along environmental gradients in continental bogs. Ecoscience **2:** 395-407.

Birks, H.J.B., Line, J.M., Juggins, S., Stevenson, A.C., and ter Braak, C.J.F. 1990. Diatoms and pH reconstruction. Philosophical Transactions of the Royal Society of London B **327:** 263-278.

Boer, G.J., Flato, G., and Ramsden, D. 2000. A transient climate change simulation with greenhouse gas and aerosol forcing; projected climate for the 21st century. Climate Dynamics **16:** 427-450.

Brown, R.J.E. 1968. Occurrence of permafrost in Canadian peatlands. Proceedings of the Third International Peat Congress, Quebec. pp. 174-181.

Camill, P. 1999. Peat accumulation and succession following permafrost thaw in boreal peatlands of Manitoba, Canada. Écoscience **6:** 592-602.

Camill, P. and Clark, J.S. 1998. Climate change disequilibrium of boreal permafrost peatlands caused by local processes. The American Naturalist **151:** 207-222.

Damman, A.W.H. 1977. Geographical changes in the vegetation pattern of raised bogs in the Bay of Fundy region of Maine and New Brunswick. Vegetatio **35:** 137-151.

Engelfield, P.G.C. 1994. Rate of permafrost degradation in peatlands. M.Sc. Thesis. University of Alberta, Edmonton, Alberta. 33 pp.

Gignac, L.D. and Vitt, D.H. 1990. Habitat limitations of *Sphagnum* along climatic, chemical, and physical gradients in mires of western Canada. The Bryologist **93:** 7-22.

Gignac, L.D., Vitt, D.H., Zoltai, S.C., and Bayley, S.E. 1991. Bryophyte response surfaces along climatic, chemical and physical gradients in mires of western Canada. The Bryologist **93:** 7-22.

Gordon, A.D. and Birks, H.J.B. 1974. Numerical methods in Quaternary paleoecology. II. Comparison of pollen diagrams. New Phytologist **73:** 221-249.

Halsey, L.A., Vitt, D.H., and Bauer, I.E. 1998. Peatland initiation during the Holocene in continental western Canada. Climatic Change **40:** 315-342.

Halsey, L.A., Vitt, D.H., and Zoltai, S.C. 1995. Disequilibrium response of permafrost in boreal continental western Canada to climate change. Climatic Change **30:** 57-73.

Heinselman, M.L. 1970. Landscape evolution, peatland types, and the environment on the Lake Agassiz Peatlands Natural Area, Minnesota. Ecological Monographs **40:** 235-261.

Hill, M.O. 1974. Correspondence Analysis: a neglected multivariate method. Applied Statistics **23:** 340-354.

Ireland, R.R., Brassard, G.R., Schofield, W.B., and Vitt, D.H. 1987. Checklist of the mosses of Canada. II. Lindbergia **13:** 1-62.

Janssens, J.A., Hansen, B.C.S., Glaser, P.H., and Whitlock, C. 1992. Development of a raised-bog complex. *In* The Patterned Peatlands of Minnesota. *Edited by* H.E. Wright, Jr., B. Coffin, and N.E. Aaseng. University of Minnesota Press, Minneapolis. pp. 189-222.

Jeglum, J.K., Rothwell, R.L., Berry, G.J., and Smith, G.K.M. 1994. New volumetric sampler increases speed and accuracy of peat surveys. Forestry Canada, Ontario Region, Technical Note No. 9. 4 pp.

Johnson, E.A. 1992. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, Cambridge.

Kuhry, P. 1998. Late Holocene permafrost dynamics in two subarctic peatlands of the Hudson Bay lowlands (Manitoba, Canada). Eurasian Soil Science **31:** 529-534.

Kuhry, P. 1997. The paleoecology of a treed bog in western boreal Canada: a study based on microfossils, macrofossils, and physico-chemical properties. Review of Paleobotany and Palynology **96:** 183-224.

Kuhry, P. 1994. The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada. Journal of Ecology **82:** 899-910.

Kuhry, P., Halsey, L.A., Bayley, S.E., and Vitt, D.H. 1992. Peatland development in relation to Holocene climatic change in Manitoba and Saskatchewan (Canada). Canadian Journal of Earth Sciences **29:** 1070-1090.

Kuhry, P., Nicholson, B.J., Gignac, L.D., Vitt, D.H., and Bayley, S.E. 1993. Development of *Sphagnum*-dominated peatlands in boreal continental Canada. Canadian Journal of Botany **71:** 10-22.

Lavoie, C. and Payette, S. 1995. Analyse macrofossile d'une palse subarctique (Quebec nordique). Canadian Journal of Botany **73:** 527-537.

Legendre, P. and Legendre, L. 1998. Numerical Ecology. Elsevier Scientific Publishing Company, Amsterdam.

Lieffers, V.J. and Rothwell, R.L. 1986. Effects of depth of water table and substrate temperature on root and top growth of *Picea mariana* and *Larix laricina* seedlings. Canadian Journal of Forest Research **16:** 1201-1206.

McCune, B. and Mefford, M.J. 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4. MjM Software Design, Gleneden Beach, Oregon, USA.

Moss, E.H. 1983. Flora of Alberta. 2nd Edition. *Revised by* J.G. Packer. University of Toronto Press, Toronto.

Nicholson, B.J. and Vitt, D.H. 1990. The paleoecology of a peatland complex in continental western Canada. Canadian Journal of Botany **68:** 121-138.

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. *In* A systems analysis of the global boreal forest. *Edited by* H.H. Shugart, R. Leemans, and G.B. Bonan. Cambridge University Press. pp. 144-169.

Prentice, I.C. 1980. Multidimensional scaling as a research tool in Quaternary palynology: a review of theory and methods. Review of Paleobotany and Palynology **31:** 71-104.

Stotler, R. and Crandall-Stotler, B. 1977. A checklist of the liverworts and hornworts of North America. The Bryologist **80:** 405-429.

ter Braak, C.J.F. 1995. Calibration. *In* Data analysis in community and landscape ecology. *Edited by* R.H.G. Jongman, C.J.F. ter Braak, and O.F.R. van Tongeren. Cambridge University Press, Cambridge. pp. 78-89.

Thie, J. 1974. Distribution and thawing of permafrost in the southern part of the discontinuous permafrost zone in Manitoba. Arctic **27:** 189-200.

Tolonen, K. 1984. Interpretation of changes in the ash content of ombrotrophic peat layers. Bulletin of the Geological Society of Finland **56:** 207-219.

Turetsky, M.R., Wieder, R.K., Williams, C., Jendro, J., and Vitt, D.H. 2000. Peat chemistry and permafrost in the boreal forest of Alberta: implications for climate change. Écoscience **7:** 379-392.

Vitt, D.H. and Andrus, R.E. 1977. The genus *Sphagnum* in Alberta. Canadian Journal of Botany **55:** 331-357.

Vitt, D.H., Bayley, S.E., and Jin, T.-L. 1995. Seasonal variation in water chemistry over a bog-rich fen gradient in continental western Canada. Canadian Journal of Fisheries and Aquatic Sciences **52:** 587-606.

Vitt, D.H., Halsey, L.A., Bauer, I.E., and Campbell, C. 2000. Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. Canadian Journal of Earth Sciences **37:** 683-693.

Vitt, D.H., Halsey, L.A., and Zoltai, S.C. 1994. The bog landforms of continental western Canada in relation to climate and permafrost patterns. Arctic and Alpine Research **26:** 1-13.

Vitt, D.H., Halsey, L.A., and Zoltai, S.C. 2000. The changing landscape of Canada's western boreal forest: the current dynamics of permafrost. Canadian Journal of Forest Research **30:** 283-287.

Vitt, D.H., Horton, D.G., Slack, N.G., and Malmer, N. 1990. *Sphagnum*-dominated peatlands of the hyper-oceanic British Columbia coast: patterns in surface water chemistry and vegetation. Canadian Journal of Forest Research **20:** 696-711.

Vitt, D.H. and Kuhry, P. 1992. Changes in moss-dominated wetland ecosystems. *In* Bryophytes and Lichens in a Changing Environment. *Edited by* J.W. Bates and A.M. Farmer. Oxford University Press, Oxford. pp. 178-210.

Vitt, D.H., Li, Y., and Belland, R.J. 1995. Patterns of bryophyte diversity in peatlands of continental western Canada. The Bryologist **98:** 218-227.

Wein, R.W. 1983. Fire behaviour and ecological effects in organic terrain. *In* The Role of Fire in Northern Circumpolar Ecosystems. *Edited by* R.W. Wein, and D.A. McLean. John Wiley and Sons, New York. pp. 81-95.

Wein, R.W. and MacLean, D.A. 1983. The Role of Fire in Northern Circumpolar Ecosystems. John Wiley and Sons, New York.

Zoltai, S.C. 1972. Palsas and peat plateaus in central Manitoba and

Saskatchewan. Canadian Journal of Forest Research **2:** 291-302.

Zoltai, S.C. 1993. Cyclic development of permafrost in the peatlands of northwestern Alberta, Canada. Arctic and Alpine Research **25:** 240-246.

Zoltai, S.C. 1995. Permafrost distribution in peatlands of west-central Canada during the Holocene warm period 6000 years B.P. Géographie Physique et Quaternaire **49:** 45-54.

Zoltai, S.C. and Tarnocai, C. 1971. Properties of a wooded palsa in northern Manitoba. Arctic and Alpine Research **3:** 115-129.

Zoltai, S.C., Morrissey, L.A., Livingston, G.P., and deGroot, W.J. 1998. Effects of fire on carbon cycling in North American boreal peatlands. Environmental Reviews **6**: 13-24.

CHAPTER 5:
GENERAL DISCUSSION

5.1 Summary and synthesis

In the mosaic of upland forest and lowland peatland in the boreal and subarctic regions of the northern Canadian prairie provinces, localized permafrost peatlands cover 17,505 km^2 of land area, or 12.7% of the total peatland area in the region shown in Figure 2-1. The results of Chapter 2 are the first that identify the landform gradient from localized permafrost to peat plateau from directly mapped landform cover data, summarize their distribution in regional maps, and explore the correlations between the gradient and environmental variables of climate and landscape. Vitt *et al.* (1994) showed that localized permafrost bogs occur widely across each of the prairie provinces, and that localized permafrost fens were less extensive in occurrence, found mostly in Manitoba. Although the frequency of the occurrence of localized permafrost fens is lower, Chapter 2 shows that they in fact cover a greater area than localized permafrost bogs (Table 2-1). This was somewhat unexpected, as permafrost is believed to have an affinity for the dry conditions of continental bogs. However, when expressed as a proportion of total bog and fen area, a greater proportion of the total bog area has localized permafrost landforms (38%) compared to the proportion of total fen area that has localized permafrost landforms (9%). This supports the idea that permafrost is most easily formed in ombrogenous peatlands (also evident in the strong correlation between the proportion of bog peatland with the permafrost landform gradient – Table 2-2), although it also shows that permafrost can form in areas that are dominated by fens. Local factors also play a large role in permafrost formation, and isolated dry brown moss hummocks in rich fens, or small areas of dry, elevated (even possibly ombrotrophic) *Sphagnum* areas in poor fens likely serve as important nucleation points during initial aggradation.

The importance of local factors is also supported by the canonical discriminant analysis that related the permafrost landform gradient (the increased southward dominance of localized permafrost peatland over peat plateau) to climate and landscape variables. Though this analysis reinforces the strong relationship between permafrost and climate that has been long documented in the literature (Brown 1960) and the affinity for extensive permafrost formation with increased bog area (mean annual temperature and the proportion of bog peatland were the two variables most strongly correlated with canonical axis 1 that best separated the permafrost classes), only 33% of the total variation was explained by the regional variables (Table 2-2). To better determine the factors that control localized permafrost development in peatlands, the scale of investigation should be larger. A higher resolution dataset that accounts for variability in landscape factors within the gridcell space used in this study (i.e. a peatland-by-peatland analysis) would perhaps be more sensitive to these local factors. However, it may also be that the present pattern of localized permafrost development is under extra-local (centimeters - meters) control by conditions that either existed in the past that cannot be measured (permafrost aggradation) or by localized disturbance events such as fire or tree blow-downs (permafrost degradation).

The study presented in Chapter 3 is the most thorough investigation of localized permafrost bog plant communities completed to date. Changes in bog plant communities due to permafrost aggradation and degradation are shown to be substantial. Permafrost formation results in an elevation of bog surfaces above the water table, the promotion of black spruce growth, and a change in ground cover from *Sphagnum*-dominated to feathermoss- or lichen-dominated over time. These plant community changes have created unique frost mound features and environments in continental bogs that are more similar vegetationally to upland black spruce stands. When permafrost melts, the frost mound surface collapses often to below the water table. Trees are drowned in

the process, wet-adapted sphagna come to dominate, and total plant diversity increases back to bog values.

Vegetation studies of bogs from across continental western Canada show that undisturbed continental bog communities are relatively predictable in that they are low in rare plants and mean alpha diversity in terms of both vascular plants (Glaser 1992) and bryophytes (Vitt and Belland 1995; Vitt *et al.* 1995). Paleoecological studies of peatland macrofossil sequences show that continental bogs can also persist for thousands of years on the landscape (Nicholson and Vitt 1990; Kuhry *et al.* 1993; Kuhry 1997). Internal lawn vegetation change is in contrast to the stability observed in bogs. Following degradation and surface collapse, initial wet communities can be replaced in relatively rapid succession by progressively drier *Sphagnum*-dominated communities. The initial communities following permafrost degradation, as well as the duration of those communities on the landscape are also variable, depending on wetness conditions in internal lawns (Chapter 4). This creates greater plant community variability both spatially and temporally in internal lawns compared to continental bogs. Modern internal lawn vegetation and surface conditions are drier than was previously thought. The high cover of *Sphagnum fuscum* in the internal lawn releves (two-thirds with greater than 50% *S. fuscum* cover, and 63% mean cover in all internal lawns) shows that the wet, treeless conditions that characterize localized permafrost collapse are of relatively short duration. Drier conditions and communities quickly succeed wetter communities as peat accumulates.

5.2 Considerations for future research

Although my field studies are the most extensive investigations of the plant communities and development of localized permafrost bogs to date, localized permafrost occurs in both bogs and fens in continental western Canada (Vitt *et al.* 1994). Additionally, in Chapter 2 I demonstrated that localized permafrost fens cover a larger area than localized permafrost bogs. Localized permafrost aggradation likely leads to similar vegetation whether localized

permafrost occurs in bogs or fens, due to the isolation of surfaces from the surrounding peatland regardless of that peatland's hydrological status. Considerable similarity exists between the frost mound vegetation described in Chapter 3 and that described from a frost mound located in a rich fen by Zoltai and Tarnocai (1971), especially in the dominant ground layer cryptogams. Localized permafrost degradation, however, creates internal lawns that are strongly affected by the hydrology of the surrounding peatland matrix, and internal lawns in localized permafrost fens are likely very different than that shown here for localized permafrost bogs. In Chapter 3, I showed that species occur in internal lawns that either do not occur or are rare in the surrounding bog matrix, due to the creation of wet, treeless, even weakly minerotrophic conditions that do not otherwise exist in continental bogs. Unique microhabitats are probably not created in fens to the degree they are in bogs following localized permafrost melt, due to movement of minerotrophic surface waters through fens and the presence of pool microhabitats in the surrounding fen matrix (regardless of their position on the poor – rich fen gradient). Peatland development following collapse is likely also different in fens, that would follow pathways of succession similar to those that occur other wet microhabitats in the fen. Regardless, degradation would still increase the amount of area covered by these wet conditions. At this time, localized permafrost fens have not been studied comprehensively. Given the extensive coverage of these peatlands in continental western Canada (Chapter 2), the ecological impacts of localized permafrost dynamics in fens need to be investigated to compliment the results in this thesis to fully understand how the region has been affected, and how it will change in the future.

The results from Chapter 2 show that the southern limit of permafrost has shifted north in the recent past due to extensive degradation of localized permafrost in peatlands. The timing of this permafrost degradation, however, and the spatial patterning of degradation events at local and regional scales remains largely unknown. Although some data exist for the age of collapse scar

formation in peat plateaus (Camill and Clarke 1998; Engelfield 1994; Thie 1974), these are limited to recent melt within the period that trees are still suitably undecomposed for dendrochonological crossdating, or the period of available aerial photographs. Dates for degradation of localized permafrost in boreal peatlands are nearly nonexistent in western Canada, although dates of compression wood initiation in black spruce from internal lawns in bogs (four trees) have been placed between 1893 and 1945 (Vitt *et al.* 1994). Although the descriptive evidence of the changes resulting from localized permafrost melt is growing, the temporal aspect of these changes is largely missing from our understanding of the response of boreal permafrost to climatic change. To better understand the changes that are likely to occur within the region, we must learn when past changes have taken place and the rate at which they have occurred. The problem of determining the extent that permafrost degrades in direct response to climatic change versus how much degrades in direct response to fire also remains unresolved. The dating of degradation events, together with paleoecological information from peat cores, would allow us to better understand when and why permafrost has melted in the past. This, in turn, would allow better predictions of how peatland ecosystems will be affected in the future as melt continues.

5.3 Literature cited

Brown, R.J.E. 1960. The distribution of permafrost and its relation to air temperature in Canada and the USSR. Arctic **13:** 163-177.

Camill, P. and Clark, J.S. 1998. Climate change disequilibrium of boreal permafrost peatlands caused by local processes. The American Naturalist **151:** 207-222.

Engelfield, P.G.C. 1994. Rate of permafrost degradation in peatlands. M.Sc. Thesis. University of Alberta, Edmonton, Alberta. 33 pp.

Glaser, P.H. 1992. Raised bogs in eastern North America - regional controls for species richness and floristic assemblages. Journal of Ecology **80:** 535-554.

Kuhry, P. 1997. The paleoecology of a treed bog in western boreal Canada: a study based on microfossils, macrofossils, and physico-chemical properties. Review of Paleobotany and Palynology **96:** 183-224.

Kuhry, P., Nicholson, B.J., Gignac, L.D., Vitt, D.H., and Bayley, S.E. 1993. Development of *Sphagnum*-dominated peatlands in boreal continental Canada. Canadian Journal of Botany **71:** 10-22.

Nicholson, B.J. and Vitt, D.H. 1990. The paleoecology of a peatland complex in continental western Canada. Canadian Journal of Botany **68:** 121-138.

Thie, J. 1974. Distribution and thawing of permafrost in the southern part of the discontinuous permafrost zone in Manitoba. Arctic **27:** 189-200.

Vitt, D.H. and Belland, R.J. 1995. The bryophytes of peatlands in continental western Canada. Fragmenta Floristica et Geobotanica **40:** 339-348.

Vitt, D.H., Halsey, L.A., and Zoltai, S.C. 1994. The bog landforms of continental western Canada in relation to climate and permafrost patterns. Arctic and Alpine Research **26:** 1-13.

Vitt, D.H., Li, Y., and Belland, R.J. 1995. Patterns of bryophyte diversity in peatlands of continental western Canada. The Bryologist **98:** 218-227.

Zoltai, S.C. and Tarnocai, C. 1971. Properties of a wooded palsa in northern Manitoba. Arctic and Alpine Research **3:** 115-129.

APPENDIX 1:
Plant community data (raw abundances) from 89 landform relevés from three localized permafrost bogs (anz = Anzac Bog, AB, pat = Patuanak Bog, SK, msl = Moose Lake, MB; see Table 3-1) in continental western Canada. CB = continental bog, FM = frost mound, IL = internal lawn. Plant community data are reported as percent cover, where 0.2 = cover less than one percent, 0.01 = one or two individual plants, 0.05 = species found outside the 5x5 m plot within a 25 m radius of the plot (see methods in Chapter 3).

APPENDIX 1:

Site	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz
Landform type	CB	CB	CB	CB	CB	CB	CB	CB	CB	CB	FM	FM	FM	FM	FM	FM	FM	FM	FM
Releve Replicate #	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9
VASCULAR PLANTS																			
Andromeda polifolia	0	0.05	0.2	1	0	1	0.05	2	0.05	1	0	0	0	0	0	0	0	0	0
Betula papyrifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Betula pumila	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex aquatilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex canescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex paupercula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex trisperma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chamaedaphne calyculata	7	0.2	2	8	5	4	3	1	4	1	0	0	0.05	0.05	0.01	0	0	0.05	0
Drosera rotundifolia	0	0.2	0	0.01	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0
Epilobium angustifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eriophorum vaginatum	2	0.2	0.2	0.2	0.2	4	0	0.2	0.2	0	0	0.01	0	0	0	0.05	0	0	0
Kalmia polifolia	2	1	3	1	2	0.05	3	2	1	0.2	0	0	0	0	0	0	0	0	0
Ledum groenlandicum	10	14	10	20	12	12	20	8	7	13	0.05	0.05	2	0.2	0.2	3	3	0.05	0.2
Picea mariana	39	12	17	57	35	32	27	28	11	26	46	42	44	57	49	35	50	40	54
Rubus chamaemorus	0.2	1	2	1	1	0.2	0.2	2	0.2	2	0.01	0.05	0.05	0.05	0	0.05	0.05	0.05	0.2
Scheuchzeria palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Smilacina trifolia	1	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0
Vaccinium myrtilloides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium oxycoccus	0.2	0.2	2	0.2	0.2	0.2	0.2	0.2	0	0.2	0	0	0.01	0.05	0	0	0	0	0
Vaccinium vitis-idaea	0	0.2	0.05	0.05	0.2	0.05	0.2	0	0	0.05	0	0	0.01	0	0.05	0.05	0.2	0.05	0
MOSSES																			
Amblystegium serpens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aulocomnium palustre	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brachythecium erhythrorrhizon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brachythecium starkei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calliergon stramineum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratodon purpureus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicranum elongatum	0	0	0.05	0	0	0	0.2	0	0	0	0	0	0.05	0.05	0.05	0.05	0	0	0.05
Dicranum flagellare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicranum fragillifolium	0.05	0	0	0	0	0.05	0.05	0.05	1	0.05	0.2	0	0.2	0.05	0.2	0.05	0.2	0.2	0.2
Dicranum fuscescens	0	0	0	0	0.2	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0
Dicranum groenlandicum	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0.05	0	0.05	0.05	0	0
Dicranum polysetum	0.2	0.2	0.2	0.2	0.2	0	0.05	0.05	0	0.2	2	5	3	3	2	2	2	4	4
Dicranum tauricum	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.05	0	0	0	0
Dicranum undulatum	2	0.2	0.2	0.2	0.2	7	1	0.2	4	0.2	0	0	0	0	0.2	0.05	0.2	0.05	1
Drepanocladus exannulatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drepanocladus fluitans	0.05	0	0	0	0.2	0.2	0.2	0	0	0	0	0.05	0.05	0	0	0	0	0	0
Drepanocladus uncinatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hylocomium splendens	0	0.01	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0
Plagiothecium laetum	0	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0.05	0.05	0
Pleurozium schreberi	15	7	4	25	40	2	25	15	0.2	30	90	48	85	93	86	63	73	52	76
Pohlia nutans	0	0	0.05	0.05	0	0.2	0.2	0.05	0	0.2	0.2	0.05	0.2	0.05	0	0	0.05	0.2	0
Pohlia sphagnicola	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polytrichum strictum	0.05	0	0	0	0	0.2	0.05	0.05	0	0	0	0	0.05	0	0	0	0	0	0.05
Ptilium crista-castrensis	0	0.01	0	0	0	0	0	0	0	0	0.2	0.01	0	0	0	0	0	0	0
Sphagnum angustifolium	10	5	5	10	15	3	40	25	15	35	0	0	0	0	0	0	0	0	0
Sphagnum balticum	0.05	0.2	0	0.05	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphagnum fuscum	50	68	73	35	18	53	17	32	64	18	0	0	0	0	0	0	0.05	0	0
Sphagnum jensenii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphagnum lindbergii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphagnum magellanicum	4	8	0.2	2	3	2	0.05	10	4	4	0	0	0	0	0	0	0	0	0
Sphagnum nemoreum	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphagnum obtusum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphagnum riparium	0.05	0	0	0	0	0.05	0.05	0	0.05	0	0	0	0	0	0	0	0	0	0
Sphagnum russowii	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0
Sphagnum squarrosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Splachnum ampullaceum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Splachnum luteum	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0
HEPATICS																			
Anastrophyllum michauxii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calypogeia muelleriana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calypogeia sphagnicola	0	0	0	0.05	0.2	0	0.2	0	0	0	0	0	0	0	0	0.05	0	0	0
Cephalozia bicuspidata	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0
Cephalozia lunulifolia	0.2	0.2	0.2	0.05	0.2	0.2	0.2	0.2	0.2	0.05	0	0	0	0.05	0	0.05	0	0.2	0
Cephalozia macrostachya	0	0	0	0	0	0	0.2	0.05	0	0	0	0	0	0	0	0	0	0.2	0
Cephaloziella hampaena	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0
Cephaloziella spinigera	0	0	0	0	0.2	0	0	0.05	0.2	0	0	0	0	0	0	0	0	0	0
Cladopodiella fluitans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidozia reptans	0.2	0.05	0	0.2	0.2	0.2	0.2	0.2	0	0.05	0	0	0	0	0	0	0	0	0
Lophozia ventricosa	0.2	0	0	0.05	0.2	0.2	0.2	0.05	0	0.05	0	0	0	0	0	0.05	0	0	0
Marchantia polymorpha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mylia anomala	2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	2	0.05	0	0	0.05	0.05	0	0	0	0.2	0
Ptilidium ciliare	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.05	1	35	3	3	6	3	5	4	7
Ptilidium pulcherimum	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0.2	0	0	0	0	0
Riccardia latifrons	0	0	0.2	0	0	0	0.2	0.2	0	0	0	0	0	0	0	0	0	0	0
LICHENS																			
Cladina mitis	7	6	15	20	23	25	8	12	6	10	0.05	1	3	0.05	6	5	10	0.05	5
Cladina rangiferina	0.05	3	1	7	2	2	3	5	2	0.2	0.2	7	2	0.05	3	20	5	0.05	2
Cladina stellaris	0	0.2	0.05	0.05	0.2	0.2	0.05	0	0	0.05	0.05	0.2	0.05	0.05	0	0.05	3	0	0
Icmadophila ericitorum	0.05	0.2	0.01	0	0	0.2	0.05	0	0.01	0.01	0	0	0	0	1	0	0	0	0
Peltigera aphosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bare Peat	6	3	0	3	1	5	7	1	2	3	7	4	4	1	6	7	2	40	5

APPENDIX 1: CONT'D

anz FM 10	anz IL 1	anz IL 2	anz IL 3	anz IL 4	anz IL 5	anz IL 6	anz IL 7	anz IL 8	anz IL 9	anz IL 10	pat CB 1	pat CB 2	pat CB 3	pat CB 4	pat CB 5	pat CB 6	pat CB 7	pat CB 8	pat CB 9	pat CB 10	pat FM 1	pat FM 2	pat FM 3
0	0.2	0.2	0	0	0.2	0.2	0.2	2	2	0	0	0	0	0	2	0.01	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	3	2	2	3	2	0	3	3	3	4	4	0.2	6	3	2	5	2	1	4	3	0	0.01	2
0	0.2	0.2	0.2	0.2	0	0.2	0.2	0.2	0.2	0	0.2	0.2	0	0	0	0.05	0.05	0.2	0	0.2	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	3	2	1	0.2	2	1	2	6	1	4	2	3	2	0.2	3	1	0.2	5	3	0	0	0	0
0	0.2	0.2	1	0.2	1	2	3	4	3	2	1	1	2	2	0	1	0	2	2	1	0	0	0
0	0.2	1	3	7	4	3	2	1	4	2	3	4	20	20	15	7	12	7	15	20	15	10	15
48	0.2	0.2	2	0.2	1	1	1	0.2	1	2	15	15	17	8	18	9	37	9	22	10	53	75	31
0.05	0.2	0.2	0.01	0	0.2	0.2	0.2	0.2	0.2	0.2	0.2	1	0	0.05	0	0	2	0.05	0.2	0.05	0.01	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	1	0.2	0	0	0.2	0	0	1	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0.2	0.2	0.2	0.2	0.2	0.2	1	1	0.2	0.2	0.2	1	3	2	1	0.2	1	1	0.2	0.2	0	0	0.2
0	0.2	0.2	0.2	0	0	0.2	0	0.2	0.2	1	0.2	0	0.05	0.05	0.05	0	0	1	0	0.2	0.01	0.2	0.05
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.2	0.05	0.05	0	0	0.2	0.2	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0.2	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0	0.2	0	0	0.05	0.2	0.2	0.05
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0.2	0	0	0	0	0	0	0	0.2	0.05	0.2	0.05	0.05	0	0.2	0.05	0.2	0	0.2	0	0.2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0.2	0	0.2	0	0	0	0.2	0	0.2	0.2	0.2	0.2	0.05	0	0.2	0.05	0.2	0.2	0.2	0	0.2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0.01	0.2	0.2	0	0.2	0	0	0.2	0.2	0	0.2	0.2	0	0	0	0.05	0	0.05	0	0	0	0	0
0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	3	0.05
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0.05	0	0	0
91	0	0	0.2	0	0	0	0	0	0	0	1	3	3	0.05	0.2	6	33	0.2	10	3	94	70	62
0.05	0.2	0.2	0	0	0.2	0	0	0	0.2	0	0.2	0	0.01	0	0.2	0.2	0.2	0.05	0.2	0.2	0.2	0.2	0.05
0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0.2	0	0	0	0	0	0	0
0	0.02	0	0.01	0	0	0.2	0.2	0	0	0	0.01	0	0.2	0.05	0.2	0.2	0	0.2	0	0	0.2	0.2	0.2
0.05	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0.01	6	0
0	2	4	12	1	3	15	7	22	31	11	20	45	7	0.2	5	3	10	2	15	1	0	0	0
0	0	0	0	0	0	0	0	0	1	0	0	0.05	0.2	0	0.05	0	0	0	0	0	0	0	0
0	81	79	77	98	93	69	89	57	33	80	78	50	67	87	86	82	41	93	67	95	0	0	7
0	0	2	0	0	0	0	0	1	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	1	5	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	15	13	4	1	3	7	3	10	20	8	1	1	0.05	0	3	2	1	0.2	0	0	0	0	0
0	0	0.2	0.2	0.2	0.2	0	0	0	0	0	0.01	0	0.05	0	0.05	0.01	0.2	0	0	0.05	0.01	0.2	0
0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	2	3	0	0	5	0	3	10	0	0.2	1	0	0	0	0	0	0	0	0	0	0	0
0	0.2	0.2	3	0.2	0.2	4	0.2	5	6	0	0	0	3	1	0	0	0	0.2	0	0	0.01	1	0.05
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0.2	0	0	0.2	0.2	0.2	0	0.2	0.2	0.2	0	0	0	0	0	0.2	0	0.05	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0.05	0	0	0.2	0.2	0.2	0.2	0.2	0	0.2	0.2	0.01	0.05	0	0.05	0.2	0.05	0.2	0.2	0.2	0.05	0	0	0.2
0	0	0.2	0	0	0.2	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0.05	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0.2	0	0	0	0	0.2	0	0	0.2	0	0	0.2	0.2	0	0	0	0	0
0	0	0	0.2	0	0	0	0.2	0.2	0.2	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0.2	0.2	0	0.2	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0.2	0	0	0	0	0	0	0.2	0.01	0.05	0	0.05	0	0	0.2	0	0.2	0.05	0	0
0.05	0	0	0	0	0	0	0	0	0.2	0.2	0.01	0.2	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0.05	0	0.2	1	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	2	2	0.2	0.2	0.2	0.2	0.2	0.2	0	0	0.05
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0.2	0.2	0.2	0.05
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2
0	0	0	0	0	0	0.2	0.2	0	0.2	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0.2	0	0	0.2	0	0	0	0	1	0.05	17	8	1	0.2	5	1	3	0.2	0.2	0.2	20
0.05	0	0	0.2	0	0	0	0	0	0	0	0.2	0.05	0	0.05	0	0	0	0.05	0.05	0	1	0	7
0.05	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0.01	0	3
0	0.01	0	0	0	0	0.01	0	0	0	0	0.2	0.01	0.2	0.01	0	0.05	0.01	0.05	0.05	0.2	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0
3	0	0	0	0	0.2	0	0	0	0	1	0	0	0	2	5	7	10	4	5	1	5	20	1

APPENDIX 1: CONT'D

pat FM 4	pat FM 5	pat FM 6	pat FM 7	pat FM 8	pat FM 9	pat IL 1	pat IL 2	pat IL 3	pat IL 4	pat IL 5	pat IL 6	pat IL 7	pat IL 8	pat IL 9	pat IL 10	msl CB 1	msl CB 2	msl CB 3	msl CB 4	msl CB 5	msl CB 6	msl CB 7	msl CB 8
0	0	0	0	0	0	0.2	0	0.2	0	0.2	0	0	0	0	0.2	0.05	0.2	0	0	0	0	0	0
0.05	0.05	0	0	0	0	0	0	0	0.2	0.2	0.2	0.2	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0.2	0.2	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0.2	0	0	0	0.2	2	0	0	0	0.2	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0.01	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0.2	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0.2	0.05	1	0.05	0.2	3	2	2	1	2	1	2	6	1	4	2	3	3	6	3	3	3	3
0	0	0	0	0	0	0.2	0.2	0.2	0	0.2	0	0	0.2	0.2	0	0.2	0.2	0.05	0	0	0	0	0
0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0.05	0	0	0	0.05	2	0.2	0.2	0.2	3	0	0.2	1	1	0	1	0.2	0.05	1	1	0.2	2	1
0	0.01	0	0	0	0	0.2	0.2	0.2	0.2	1	0.2	0.2	0.2	0.2	0.2	1	1	4	4	5	4	4	4
1	8	8	12	6	8	0.2	0.2	0.2	0.2	0.2	0.2	1	1	0.2	1	7	3	1	4	1	0	3	0
49	37	55	52	40	49	2	1	1	0.2	0.2	0.2	0.2	1	0.2	0.2	16	15	6	15	16	13	15	20
0	0.2	0.05	0.05	0.05	0.2	0.2	0.2	0	0.2	0.2	0.2	0.2	0.2	0.2	0	0.2	0.2	1	1	0.2	0	1	0.2
0	0	0	0	0	0	0.2	0.2	0.2	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	3	5	0.2	1	0.2	2	1	0	0	0	0	3	0	0	1	0	0
0	0.2	0.05	0.05	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0
0.05	0.2	0.05	0	0.05	0	0.2	1	0.2	0.2	0.2	1	0.2	0.2	0.2	0.2	0.2	0.2	0	1	1	1	1	1
0.2	0.2	0.2	0	0.2	0	0	0.01	0.2	0	0	0.2	0.2	0.2	0	0	1	0.2	1	2	1	0	0.2	0.2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0.2	0	0	0.2	0	0.2	0	0	0.2	0	0	0	0	0	0	0	0.2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0.05	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0.05	0.05	0.05	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	1	1	1	1	0	0	0	0	0	0	0.2	0	0	0	0.2	0	0	0.2	0.2	0	0.05	0.2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0.05	0.05	0.2	0.2	0.2	0.05	0	0	0	0	0	0	0.2	0	0	0	0.2	0.2	0.01	0.2	0.05	0	0.05	0.2
0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0.2	0	0.2	0	0.2	0.2	0.2	0	0	0.05	0.2	0.05	0.2	0.05	0	0.05	0.05
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0.2	0.2	0.05	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0.2	0.2	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	29	93	93	88	80	0	0.2	0	0	0	0	0	0	0	0	1	0.2	0	10	0	0	1	0.05
0.05	0	0.2	0	0	0.2	0	0.2	0.2	0.2	0.2	0.2	0	0.2	0	0.2	0.2	0.05	0.05	0.2	0.2	0.2	0.05	0.2
0	0	0	0	0	0	0	0	0	0	0	0.2	0.2	0	0.2	0	0	0	0	0	0	0	0	0
0	0.2	0	0	0	0.2	0.2	0.2	0	0	0.2	0.2	0.2	0.2	0.01	0	0	0	0.05	0	0	0	0.05	0
1	0	0.2	0.2	0.2	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0.2	0	0	2	56	54	68	30	35	50	87	59	32	89	0	0	1	20	15	25	0.05	0
0	0	0	0	0	0	0.01	0.2	2	10	0	0	0	0	0	0.2	1	0	0	0.2	0	0	0	0
0.05	20	1	0	0.05	1	30	25	20	30	10	20	10	20	60	1	95	95	98	65	84	70	89	94
0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0
0	0	0	0	0	0	10	15	10	10	5	8	1	20	5	10	0	0.2	0.01	2	1	5	0	0.05
0	0	0	0	0	0	0	0.2	0	0.2	0	0.2	0	0.2	0.2	0	0	0	0	0.2	0	0	0	0.05
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	4	0	19	50	22	2	1	0	0	0.05	1	0	0	0	0.05	0.05	0.05
0.05	0	0	0	0	0	0	2	0	1	0	0.2	0	0.2	0.2	0	0.05	0.2	0.2	0	0.05	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0.2	0	0	0.2	0	0.2	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0.2	0.2	0.2	0	0.2	0.2	0	0.2	0.2	0.2	0	0	0.2	0.2	0	0.2	0	0.05
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05
0	0	0	0	0	0.2	0	0.2	0	0	0	0.2	0	0	0.2	0.2	0.2	0.2	0.05	0.2	0.05	0	0.2	0.05
0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0.2	0	0	0.2	0	0.2	0	0.2	0.2	0.05	0	0	0	0	0.2	0	0.05
0	0	0	0	0	0	0.2	0	0.2	0	0	0	0	0	0.2	0.2	0	0	0	0	0.05	0	0	0
0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0.05	0.2	0	0.2	0.05	0	0.2	0.05
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0.2	0	0.2	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0
0	0.2	0.05	0.05	0.05	0.2	3	0.2	0.2	0	0.2	0.2	0	0	2	0.2	0.2	0.2	0.2	0.2	0.05	0.2	2	2
0.2	0	0	0.05	1	0.2	0	0.2	0	0	0	0	0	0	0	0	0.2	0.2	0	0	0	0	0.05	0
0.2	0.2	0.2	0.2	0.2	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0.2	0.05	0
0.05	40	3	3	2	0.2	0.2	0.2	0.2	0	0.2	0	0.2	0	0.2	0	0.2	0.2	0.05	2	0	0	4	0.2
0.05	6	1	3	1	1	0	0	0	0	0	0	0	0	0	0	3	4	0.05	0.2	0.05	0	3	1
0	3	0.05	0.05	0.05	0.2	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0.05	0	0	0
0	0.2	0.05	0	0	0	0.01	0	0.2	0	0	0	0	0	0	0	0.01	0.2	0	0	0.2	0	0	0.05
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	1	1	0.2	7	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3

APPENDIX 1: CONT'D

msl CB 9	msl CB 10	msl FM 1	msl FM 2	msl FM 3	msl FM 4	msl FM 5	msl FM 6	msl FM 7	msl FM 8	msl FM 9	msl FM 10	msl IL 1	msl IL 2	msl IL 3	msl IL 4	msl IL 5	msl IL 6	msl IL 7	msl IL 8	msl IL 9	msl IL 10
0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0.2	0	0	0.2	0.2	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	3	2	1	7	5	2	3	2	3	2	3	3	2	2	3	4	1	0	1	2	3
0	0	0	0.01	0	0	0	0	0	0	0	0	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0.05	2	0	0.2	0.2	0	0	0	0.05	0	0	0	1	1	1	0.2	2	0.2	1	0.2	2	1
3	4	0	0.05	0	0	0.2	0	0	0	0	0	1	2	1	1	0.2	2	2	1	0.2	1
4	2	25	20	20	15	0	15	8	14	4	7	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.01	2	1
27	15	35	12	52	36	50	45	47	32	55	70	1	1	1	1	3	1	1	0.2	0.2	0.2
1	0.01	1	1	3	1	4	1	0.2	1	0.2	0.2	1	0.2	1	1	2	0.2	2	1	2	0.2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	2	0.2	0	0.01
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	0.2	0.01	0.2	0.05	0	0.05	0	0	0.05	0.05	0.2	0.2	0.2	0.2	0.2	0.2	0.2	1	2	0.2
0	0.2	0.2	0.05	0.2	0.2	0.05	0.2	1	0	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0	0	0	0	0.2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 2:
Plant community data (raw abundances) from 150 internal lawn quadrats from three localized permafrost bogs (anz = Anzac Bog, AB, pat = Patuanak Bog, SK, msl = Moose Lake Bog, MB; see Table 3-1) in continental western Canada. Plant community data are reported as percent cover, where 0.2 = cover less than one percent, and 0.01 = one or two individual plants (see methods in Chapter 3).

APPENDIX 2:

Site	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz
Internal Lawn #	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	3
Quadrat #	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1
VASCULAR PLANTS																					
Andromeda polifolia	0	0.2	5	0.2	0.2	0.2	0	0.2	0	1	0.2	0.2	2	2	2	1	2	2	0.2	1	0.2
Betula papyrifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Betula pumila	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex aquatilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex canescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex paupercula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex trisperma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chamaedaphne calyculata	3	1	1	5	0.2	3	2	0.2	12	0	2	0.2	0	1	0.2	0.2	0.2	1	1	2	7
Drosera rotundifolia	0.2	0.2	0.2	0	0.2	0	0.2	0	0	0	0.01	0.01	0	0.2	0.2	0	0.2	0.2	0	0.2	0
Epilobium angustifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eriophorum vaginatum	1	1	0.2	1	2	1	1	1	1	0.2	0.2	0	0	0	0.2	0	0	0	0	0.2	0.2
Kalmia polifolia	0.2	0.2	0.2	1	0.2	1	4	3	1	0.2	0.2	2	1	0.2	0.2	0.2	0.2	0.2	1	0.2	0.2
Ledum groenlandicum	0.2	2	0	0	1	2	0	0.2	0.2	9	0.2	0.2	0	0	0	0	0	0	0	0	0.01
Picea mariana	0.2	0.2	0.2	0.2	2	0.2	2	0.2	1	0	0.2	0.2	0.2	0	0	0	1	1	1	0.2	0.01
Rubus chamaemorus	0.2	2	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scheuchzeria palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Smilacina trifolia	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0.2	1	0.2	0.2	0.2	0.2	0.2
Vaccinium myrtilloides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium oxycoccus	0.2	1	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	1	1	0.2	0.2	0.2	0	0.2	0.2	0.2	0.2
Vaccinium vitis-idaea	0.2	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0
MOSSES																					
Amblystegium serpens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aulocomnium palustre	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brachythecium erhythrorrhizon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brachythecium starkei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calliergon stramineum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratodon purpureus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicranum elongatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicranum flagellare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicranum fragilifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicranum fuscescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicranum groenlandicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicranum polysetum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicranum tauricum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicranum undulatum	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drepanocladus exannulatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drepanocladus fluitans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0
Drepanocladus uncinatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hylocomium splendens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiothecium laetum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleurozium schreberi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pohlia nutans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pohlia sphagnicola	0.2	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0
Polytrichum strictum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ptilium crista-castrensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphagnum angustifolium	1	0	5	0.2	6	20	1	0	45	15	5	3	0.2	3	23	2	3	68	2	6	3
Sphagnum balticum	0	0	0	0	0	0.2	0	0	0	0	0	0	0.01	0.2	3	0	0	0	0	0	0
Sphagnum fuscum	97	82	81	94	92	60	99	94	50	85	91	94	99	93	50	97	82	6	96	71	97
Sphagnum jensenii	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0.2	0	0	0	0	0	0	0
Sphagnum lindbergii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphagnum magellanicum	2	3	10	6	2	20	0.2	6	5	0.2	4	3	0	4	5	1	8	26	2	17	0.2
Sphagnum nemoreum	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Sphagnum obtusum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphagnum riparium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	0	6	0	0	0	0
Sphagnum russowii	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0.2	0	0	0	0	0	0	0
Sphagnum squarrosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Splachnum ampullaceum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Splachnum luteum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HEPATICS																					
Anastrophyllum michauxii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calypogeia muelleriana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calypogeia sphagnicola	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0.2	0	0
Cephalozia bicuspidata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cephalozia lunulifolia	0	0	0.2	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0.2	0	0.2	0
Cephalozia macrostachya	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cephaloziella hampaena	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cephaloziella spinigera	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0.2	0.2	0
Cladopodiella fluitans	0	0.2	0	0	0.2	0	0	0	0	0	0	0	0	0.2	0.2	0	1	0.2	0	1	0
Lepidozia reptans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lophozia ventricosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Marchantia polymorpha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mylia anomala	0.2	13	4	0.2	0.2	0.2	0	0	0	0.2	1	0.2	0.2	0.2	1	0	1	1	0.2	5	0
Ptilidium ciliare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ptilidium pulcherimum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Riccardia latifrons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LICHENS																					
Cladina mitis	0	0.01	0	0.2	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0
Cladina rangiferina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cladina stellaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Icmadophila ericitorum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peltigera aphtosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bare Peat	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 2: CONT'D

anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz
3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5
2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7
0	0.2	2	0	1	1	0	0.2	0	0.2	0.2	0.2	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0.01
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 2: CONT'D

anz	anz	anz	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat
5	5	5	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3
8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	1	0.2	0	2	0.2	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0

APPENDIX 2: CONT'D

pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat
3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5
4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9
0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	2	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0.01	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0.2	1	0	2	2	0.2	0.2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	3	3	2	0	4	10	3	10	5	3	4	3	25	0.2	3	0	0	0	0	0.2	0	0	0	0
0	0.2	0	0.2	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	4	2	0.2	1	0	1	2	4	1	1	2	2	1	3	3	1	1	1	3	3	2	1	0	1	5
0.2	0.2	0.01	2	0.2	3	2	1	1	2	0	2	0.2	1	1	1	1	0.2	0	1	1	1	1	0	0	0.2
0	0.2	0.2	0.2	0	0	0	0	3	0	0	0	0.01	0.2	2	2	1	2	0	1	0.01	3	0.2	2	0	5
0	0	0	0	0	0	0.2	5	5	0	2	0.2	3	0.2	10	10	0	0	0	0.2	0	1	0	1	0	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0
0.01	0.2	0.2	0.2	0.01	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0.2	0	0.2	0	0.2	3	7	3	2	0	0.2	2	0	1	0	0.2	0.2	0.2	0	0	0	1	0	0	0.01	4
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0.2	2	1	1	1	2	2	1	1	1	2	1	0.2	1	0.2	0.2	1	1	0	2	1	1	1	1	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0.2	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	1	0.2	0	0.2	0	0	0.2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 2: CONT'D

pat	msi	msi	msi	msi	msi	msi	msi	msi	msi	msi	msi	msi	msi	msi	msi	msi	msi	msi	msi	msi	msi	msi	msi	msi	msi
5	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3
10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5
0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0

APPENDIX 2: CONT'D

msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl
3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5
6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
0	0	0	0	0	0	0	0	0	0	0.2	0.2	0	0	0	0	0	0	0	0	0.2	0	0.2	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 3:

Physical peat and macrofossil raw data from 18 internal lawn peat cores extracted from three localized permafrost bogs (anz = Anzac, AB, pat = Patuanak, SK, msl = Moose Lk, MB; see Table 3-1) in continental western Canada. Physical peat and macrofossil analyses were conducted on separate subsamples from each sample taken at the depth given in the data that follows (see methods in Chapter 4). Macrofossil data are reported as percent abundance, where 0.5 indicates abundance < 1%, and 0.01 indicates the presence of that macrofossil component, but at very low abundance (single leaf, small root segment, single *Sphagnum* branch, etc.).

APPENDIX 3:

Site	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz
Internal Lawn #	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2
Core Location	wet	wet	wet	wet	wet	wet	dry	dry	dry	dry	dry	dry	dry	dry	wet	wet
Sample #	1	2	3	4	5	6	1	2	3	4	5	6	7	8	2	3
Depth (cm below surface)	48.5	43	35	25	15	5	62	59	54	45	35	25	15	5	59	56
Bulk Density (mg/cc)	129.40	38.84	27.66	30.82	38.70	29.84	140.06	53.58	50.42	59.10	40.62	50.74	35.66	51.26	61.68	109.80
% Ash (w/w)	3.31	3.30	1.59	1.49	1.34	1.86	2.67	1.61	1.07	2.91	1.48	1.50	1.07	1.17	2.30	3.46
150:500 Ratio	0.29	0.26	0.15	0.05	0.03	0.01	0.38	0.33	0.30	0.31	0.09	0.09	0.09	0.08	0.13	0.17
Picea needles	0.5	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0.01	1
Picea cones	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Picea wood	1	0.5	0	0	0	0	0.5	0	0	0	0	0	0	0	0.5	0.5
Picea bark	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0.01	2
Picea twigs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleurozium schreberi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hylocomium splendens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polytrichum strictum	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	7
Dicranum spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lichen	20	0	0	0	0	0	35	0	0	0	0	0	0	0	0	5
Charcoal	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0
Ericaceous leaves	0	0	0	3	0.01	0.5	0.01	0	0.01	5	0	1	0.01	0.5	0	0.5
Ericaceous stems	0	0	0	0	0	0	5	0	0	1	0.01	1	0	0	0	10
Picea roots	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	15	2
Ericaceous roots	50	0	30	27	19	10	53	1	0.5	35	7	3	5	5	0	49
Graminoid roots	0	0	0	0.01	0	1	0.01	0.5	0.01	1	0	0	0	0	0	0
Cyperaceae epidermis	1	0.5	1	0	0	1	1	0.5	2	0.5	0.5	0.5	0	0	7	1
Carex achenes	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0
Scheuchzeria palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus chamaemorous	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drepanocladus spp.	0.01	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5
Sphagnum riparium	0	0	0	0	0	0	0	98	0	0	0	0	0	0	0	5
Sphagnum lindbergii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphagnum jensenii/majus/obtusum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphagnum angustifolium	0	0	4	0	0	0	0	1	93	58	0.5	0.5	0.01	0	23	0
Sphagnum nemoreum	0	49	15	0.01	1	0	0	0	0	0	0	0	0	0	0	0
Sphagnum magellanicum	2	45	50	70	80	50	0	0	5	0	93	25	0.5	2	10	5
Sphagnum fuscum	0	5	0	0	0	30	0	0	0	0	0	70	95	93	0	0
Pohlia nutans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mylia anomala	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0
Liverwort (unidentified)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Debris	7	0	0	0	0	0	5	0	0	0	0	0	0	0	45	8

APPENDIX 3: CONT'D

anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz	anz
2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3
wet	wet	wet	wet	wet	wet	dry	dry	dry	dry	dry	dry	dry	dry	wet	wet	wet	wet	dry
4	5	6	7	8	9	1	2	3	4	5	6	7	8	2	3	4	5	1
52	45	35	25	15	5	62	59	55	45	35	25	15	5	30	25	15	5	46
43.18	50.24	47.26	31.44	81.42	39.28	116.44	52.62	52.52	46.08	40.52	31.18	29.34	28.40	107.00	40.50	45.60	25.70	131.74
1.53	1.75	1.10	1.02	1.03	1.32	7.71	1.44	1.52	2.59	1.63	1.60	1.36	1.48	1.64	1.43	1.36	1.32	2.23
0.28	0.11	0.10	0.14	0.10	0.04	0.12	0.10	0.07	0.05	0.26	0.09	0.03	0.02	0.08	0.15	0.03	0.03	0.27
0	0	0	0	0	0	0	30	0	0	0	0	0	0	0.01	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	7	0	15	10	0	0	0	0	0	0	40	0	0	0	13
0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0
0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	15
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0.01	1	2	0.01	3	1	0	1	0	0.5	0.5	0.01	0	0	4	5	0	4	0
0	0.01	2	0	0	1	0	1	0	1	0.5	1	1	1	1	3	0	0	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	35
0.01	10	4	20	38	8	15	5	5	3	27	5	2	7	10	10	13	3	16
0	0	0	0	2	0	2	0.01	0.01	0.01	1	3	0	0	0	0	0	0	0
1	2	0.5	0.5	0.5	2	3	0	0.01	0	0	0	0	0	5	5	0	0	5
0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	1	0	0
8	50	10	0	0	0	0	0	0	0	1	0	0	0	0	0	0	10	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0
90	37	12	2	10	3	0	0	0	0	1	0	7	0	0	5	0	30	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
1	0	0	28	0	0	0	0	0	0	30	91	30	2	25	60	2	0	0
0	0	70	50	40	85	0	43	95	96	40	0	60	90	0	0	70	45	0
0	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	40	0	0	0	0	0	0	0	0	0	0	0	10

APPENDIX 3: CONT'D

anz	anz	anz	anz	anz	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat
3	3	3	3	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1
dry	dry	dry	dry	dry	wet	wet	wet	wet	wet	wet	wet	wet	dry	dry	dry	dry	dry	dry
2	3	4	5	6	2	3	4	5	6	7	8	9	1	2	3	4	5	6
42	36	25	15	5	65	55	45	35	28	25	15	5	85	82	75	65	52	45
54.40	46.90	43.62	36.74	23.74	71.44	29.62	44.20	42.42	37.36	34.52	29.38	13.40	78.20	32.02	44.94	26.28	45.02	47.30
1.65	2.05	1.65	1.58	1.43	4.45	1.35	3.12	2.69	1.86	2.03	2.72	2.69	2.17	1.69	1.20	2.05	2.40	2.16
0.14	0.22	0.24	0.04	0.04	0.26	0.18	0.21	0.27	0.24	0.19	0.17	0.07	0.16	0.23	0.13	0.13	0.20	0.39
0	0	0	0	0	0.5	0	0	0	0	0	0	0	2	0.5	0	0.01	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0.5	0	0	0	0	0	0	0	0	1	0	0	0	0
0	0	0	0	0	0.5	1	0	0.01	0	0	0	0	1	0	7	1	0	0
0	0	0	0	0	0	0.5	0	0	0	0	0	0	3	0	0	2	1	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0
0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0
0.01	2	0.5	0.5	2	0	2	2	1	0.5	1	2	1	2	2	0.5	3	2	2
5	3	0	1	0	0	2	0.01	0	1	0	0.5	0	0	0	0.01	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0
3	20	10	5	2	0	5	1	1	0.5	8	25	1	23	2	0.01	10	0.01	16
1	0	0	0	0	0	0.01	0	0	0.01	0	0.01	0	0	0	0	0	0	0.01
2	0.5	0.5	1	0	1	5	15	8	10	9	15	20	54	0.5	1	0	0.5	0.5
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	3	4	1	3	5	0.5	0.5	1	0	0	0	0	0	0
0	0	0	0	0	60	72	71	29	70	81	58	77	0	3	3	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0
82	5	0	0	0	36	10	10	55	14	1	0	0	0	55	29	5	92	79
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0.01	35	60	79	5	3
0	70	74	93	91	0	0	0	2	0	0	0	0	0	0	0	0	[illegible]	0
0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	5	0.5	0	0	0	0	1	0	0	0	0	5	0	0	0	0	0

APPENDIX 3: CONT'D

pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat
1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
dry	dry	dry	dry	wet	wet	wet	wet	wet	wet	wet	dry	dry	dry	dry	dry	dry	dry	dry
7	8	9	10	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
35	25	15	5	53	55	47	35	26	13	7	79	74	64	57	45	35	25	15
33.20	32.56	38.72	26.46	61.88	49.34	35.18	36.52	51.94	24.40	15.22	102.06	68.88	52.58	51.30	36.36	66.98	36.54	36.32
1.75	2.15	1.39	1.97	3.17	3.53	1.82	1.04	1.23	1.48	2.37	1.35	1.13	1.07	1.01	1.76	1.37	1.86	1.98
0.12	0.19	0.08	0.05	0.57	0.66	0.31	0.20	0.17	0.10	0.11	0.37	0.14	0.18	0.22	0.09	0.21	0.22	0.07
0	0	0	0	0	1	0	0	0	0	0	0	0.01	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	15	1	0	0	0	0	0	0
0	0	0	0	0	3	0	0	0	0	0	40	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0.5	0.5	0.01	0	0	0	0.01	0	1	1	0.01	10	0	0	0.5	1	1	4
2	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	3	3	3
0	0	0	0	0	0	0	0	0	0	0	31	0	0	0	0.5	0	0	0
10	15	12	8	0	2	0	8	0	0	0	0	4	0.5	8	15	20	20	22
0	0.01	0	0	5	0	0	0	0	0	0	0	0	0	0	1	1	0	0
0	0	0	0	7	5	0	5	3	0.5	0	1	3	7	10	0.5	30	5	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	3	2	20	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	40	37	70	76	85	75	98	0	15	3	3	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	62	0	2	40	50	10	10	12	24	0	0	20	70	79	13	40	30	70
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66	20	15	5	0	0	0	0	0	0	0	0	45	20	0	70	5	41	0
10	2	73	85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0

APPENDIX 3: CONT'D

pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	pat	msl	msl	msl	msl
2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	1	1	1	1
dry	wet	wet	wet	wet	wet	wet	dry	dry	dry	dry	dry	dry	dry	dry	wet	wet	wet	wet
9	2	3	4	5	6	7	1	2	3	4	5	6	7	8	2	3	4	5
6	58	45	35	25	14	7	61	59	52	47	36	25	15	6	42	37	25	15
16.72	56.20	57.46	50.56	44.02	44.66	19.82	90.02	47.72	51.76	49.02	43.84	38.98	20.12	22.38	56.58	50.76	34.46	27.90
1.32	2.28	2.58	2.69	2.82	1.56	2.02	6.13	2.81	1.89	3.71	2.42	1.80	2.58	2.59	3.89	3.31	1.68	2.72
0.04	0.18	0.23	0.23	0.12	0.14	0.01	0.11	0.11	0.19	0.11	0.14	0.14	0.04	0.03	0.32	0.23	0.10	0.07
0	0	0	0	0.01	0	0	1	0	0.01	0	0	0	0	0.5	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	5	0	0	0	0	0	1	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	1	0	0	0	0.01	0	0	0.5	0	15	0.01	0.01	0.01	0.01
7	0	0	1	0	0	0	0	0	0	0	1	3	1	0	2	0	2	0
0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0
10	0	1	7	1	7	0	5	15	5	0	12	25	30	5	20	16	20	10
0	2	0.5	3	2	0	0.01	15	7	2	2	1	0.5	0	0	4	4	0	0
0	13	10	12	40	0	0	15	10	15	5	1	0	0.01	0	3	2	13	0.5
0	0	0.01	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	85	89	77	57	92	100	1	3	78	93	35	51	0	0	70	20	1	0
0	0	0	0	0	0	0	0	55	0	0	0	0	0	0	0	10	0	0
0	0	0	0	0	0	0	27	0	0	0	50	20	69	79	1	40	24	70
79	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40	20
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	8	0	0

APPENDIX 3: CONT'D

msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl
1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2
wet	dry	dry	dry	dry	dry	dry	dry	wet	wet	wet	wet	wet	wet	dry	dry	dry	dry	dry
6	1	2	3	4	5	6	6	2	3	4	5	6	7	1	2	3	4	5
5	52	48	42	35	26	15	5	52	45	35	25	15	6	57	48	45	35	23
32.02	74.98	51.10	49.92	32.28	30.88	30.14	22.70	38.56	48.60	49.66	40.50	35.14	28.76	72.30	40.44	51.04	47.32	43.90
2.25	1.73	1.45	4.01	2.29	2.33	3.92	1.76	2.28	1.44	2.05	1.48	1.65	2.09	1.47	1.14	1.21	4.06	2.51
0.03	0.14	0.12	0.18	0.12	0.15	0.08	0.05	0.10	0.13	0.04	0.15	0.07	0.05	0.18	0.14	0.15	0.20	0.10
0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0.5	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0.5	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	3	1	3	0	0.01	2	2	2	0.5	1	1	1	0.5	1	1	0	5
1	5	0.01	0	1	0	1	0	0	0	0	0	0	2	0	0	0	0	2
0	15	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0
10	2	10	25	12	5	12	12	6	5	0	7	4	15	10	10	10	22	7
0	0.5	0	0.5	0	0	0	0	1	2	0	0	0	0	0.5	0.5	1	1	0
2	3	4	4	0	1	0	0	15	40	80	1	0	0	5	2	1	0	0
0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	0	83	55	14	0	0	0	0	0	0	10	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	74	51	20	80	95	82	0	20	15	51	0
70	0	0	15	0	0	0	4	0	0	0	1	0	0	0	0	0	0	0
0	70	0	0	70	94	87	80	0	0	0	0	0	0	51	65	72	25	86
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	3	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0

APPENDIX 3: CONT'D

msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl	msl
2	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
dry	dry	wet	wet	wet	wet	wet	wet	wet	dry	dry	dry	dry	dry	dry	dry	dry
6	7	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	9
15	6	63	57	45	35	25	15	6	73	67	62	54	45	33	25	15	6
32.40	33.32	37.48	44.34	33.66	33.28	37.18	30.32	19.76	163.06	44.68	51.82	64.64	36.86	34.34	33.24	37.64	29.24
1.79	1.02	1.12	1.26	4.28	2.10	2.58	2.51	1.82	9.03	1.39	2.01	1.86	1.68	1.81	1.50	1.49	1.71
0.05	0.05	0.21	0.20	0.13	0.08	0.29	0.06	0.05	0.22	0.18	0.17	0.11	0.18	0.14	0.07	0.03	0.04
0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	25	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	25	0	0	0	0	0	0	0	0
4	3	5	0	0	1	2	2	0	0	0	7	5	2	1	1	0	0.01
0	0	0	0	0	0	0	0	0	1	0	2	3	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	3	1	2	10	20	25	20	23	0	7	7	15	7	5	6	4	5
0	0	2	4	5	3	5	2	0	0	0	0	0	0	0	0	0	0
1	0.5	20	1	20	5	0.5	0	0	15	10	2	2	1	1	1	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	51	73	20	5	15	0	4	0	66	82	65	20	0	0	0	0
0	0	21	0	45	16	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	20	0	50	53	74	72	0	0	0	10	30	5	0	2	0
90	94	0	0	0	0	0	0	0	13	15	0	0	40	88	92	94	95
0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0